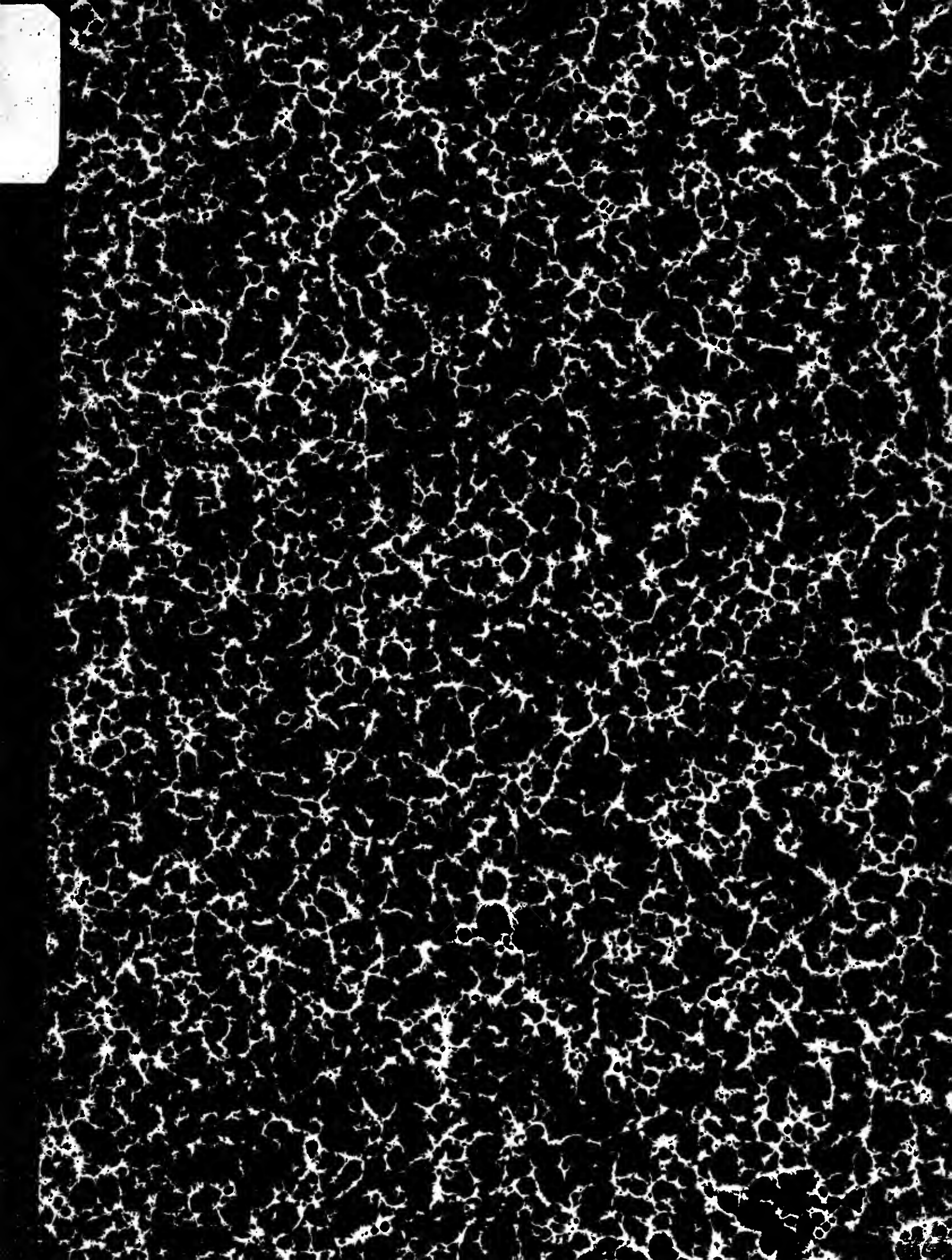

Memoirs from the Biological Laboratory
OF THE
JOHNS HOPKINS UNIVERSITY
IV, 1
WILLIAM K. BROOKS, EDITOR

THE CUBOMEDUSÆ

A DISSERTATION PRESENTED FOR THE DEGREE OF DOCTOR OF PHILOSOPHY, IN THE JOHNS HOPKINS UNIVERSITY, 1897

BY

FRANKLIN STORY CONANT

A MEMORIAL VOLUME

BALTIMORE
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BALTIMORE, MD., U. S. A.

With the kind regards of
Franklin Sloy Conard

FRANKLIN STORY CONANT

SEPTEMBER 21, 1870—SEPTEMBER 13, 1897

A BIOGRAPHICAL SKETCH

This Treatise is printed after the author's death, as a Memorial by his friends, fellow-students and instructors, with the aid of the Johns Hopkins University. It consists of his Dissertation, reprinted from the copy which was accepted by this University at his examination for the degree of Doctor of Philosophy in June, 1897.

As he had made many notes on the embryology of the Cubomedusæ, and had hoped to complete and publish them together with an account of physiological experiments with these medusæ, he had described the Dissertation on the title-page as Part I, Systematic and Anatomical, and he went to Jamaica immediately after his examination to continue his studies and to procure new material, and he there lost his life.

Franklin Story Conant was born in Boston on September 21, 1870, and he died in Boston on September 13, 1897, a few days after his arrival from Jamaica, where he had contracted yellow fever through self-sacrificing devotion to others.

He was educated in the public schools of New England; at the University of South Carolina; at Williams College, where he received the degree of Bachelor of Arts in 1893; and in the Johns Hopkins University, where he received the degree of Doctor of Philosophy in 1897, and where he was appointed a Fellow in 1896 and Adam T. Bruce Fellow in 1897.

Most of his instructors have told us that they quickly discovered that Conant was a young man of unusual intelligence and energy and uprightness, and as his education progressed he secured the esteem and the affectionate interest of all who had him in charge, so that they continued to watch his career with increasing pride and satisfaction.

He entered the Johns Hopkins University in the spring of 1894, and at once joined the party of students in zoology who were working, under my direction, in the marine laboratory of the University at Beaufort, North Carolina; and from that time until his death he devoted himself continually, without interruption, to his chosen subject—spending his winters in the laboratory in Baltimore, and devoting his summers to out-of-door studies at Beaufort and at Wood's Holl, and in Jamaica.

It is as a student and not as an investigator that we must remember Conant, for most of his time was given to reading and study on subjects of general educational value; although he had begun, before his death, to make original contributions to science and to demonstrate his ability to think and work on independent lines.

His study of the Chaetognaths was undertaken only for the purpose of verifying the account of their anatomy and development in the text books, but it soon showed the presence at Beaufort of several undescribed species. Without interrupting his more general studies, he employed his odd moments for three years in their systematic analysis, and at last published two papers, "Description of Two New Chaetognaths," and "Notes on the Chaetognaths," which show notable power of close and

accurate observation and of exact description; and, while short, are valuable contributions to our knowledge of this widely distributed but difficult group.

As he appreciated the value to one who has devoted himself to zoology of thorough acquaintance with physiological problems and the means for solving them, he wished, after he had completed his general course in physiology, to attempt original research in this field; and, at the suggestion of Professor Howell, he, in company with H. L. Clark, his fellow student, undertook and successfully completed an investigation of which Professor Howell gives the following account:

> In connection with Mr. H. L. Clark, Mr. Conant undertook to investigate the character of the nervous control of the heart beat in decapod crustaceans. They selected the common edible crab, Callinectes hastatus, and made a series of most careful experiments and dissections which resulted in proving the existence of one inhibitory nerve and two accelerator nerves passing to the heart on each side from the thoracic ganglion. They not only demonstrated the physiological reaction of these nerves, but traced out successfully their anatomical course from the ganglion to the pericardial plexus. It seemed hardly probable from an a priori standpoint that in an animal like the crab there should be any necessity for an elaborate nervous mechanism to regulate the beat of the heart, but their experiments placed the matter beyond any doubt, and have since served to call attention to this animal as a promising organism for the study of some of the fundamental problems in the physiology of the heart. As compared with previous work upon the same subject it may be said that their experiments are the most definite and successful that have yet been made.

His chief completed work, the Dissertation on The Cubomedusæ, is here printed; and through it the reader who did not know Conant must decide whether he was well fitted, by training and by natural endowments, for advancing knowledge. I myself felt confident that the career on which he had entered would be full of usefulness and honor. I was delighted when he was appointed to the Adam T. Bruce Fellowship, for I had discovered that he was rapidly becoming an inspiring influence among his fellow students in the laboratory, and I had hoped that we might have him among us for many years, and that we might enjoy and profit by the riper fruits of his more mature labors.

Immediately after his examination for the degree of Doctor of Philosophy in June, 1897, he set out for Jamaica to continue his studies at the laboratory which this University had established for the summer at Port Antonio, and he there worked for nearly three months on the development, and on the physiology of the sense-organs, of the Cubomedusæ.

His notes and specimens are so complete that I hope it will be possible to complete in Baltimore, at an early day, the work which he had expected to carry on this year.

After the sudden and alarming death of the director of the expedition, Dr. J. E. Humphrey, Conant took the burden of responsibility upon himself, and while he fully appreciated his own great danger, he devoted himself calmly and methodically to the service of others who, in their afflictions, needed his help, and he fell in the path of duty, where he had always walked, leaving behind him a clear and simple account of all the business of the laboratory and of his scientific work, and of his own affairs, complete to the day before his death.

Immediately after the opening of the University in October his friends and companions and instructors assembled to express the sorrow with which they had heard the sad news of his death, and to record their love and esteem for the generous, warm-hearted friend who in all the relations of life had proved himself so worthy of their affectionate remembrance. At this meeting those who had worked at his side in our laboratories recalled his steadfast earnestness in the pursuit of knowledge, and the encouragement they had found in his bright example; while those who had been his instructors spoke of him as one who had bettered their instruction and enriched all that he undertook by sound and valuable observations and reflections. While all united in mourning the untimely loss of one who had shown such rich promise of a life full of usefulness and honor and distinction, it was pointed out with pride that his end was worthy of one who had devoted it to the fearless pursuit of truth, and to generous self-sacrifice and noble devotion to others; and it was resolved, "That we prize the lesson of the noble life and death of Franklin Story Conant."

LIST OF THE PUBLISHED BIOLOGICAL PAPERS OF FRANKLIN STORY CONANT.

1. Description of Two New Chaetognaths. Johns Hopkins University Circulars, No. 119, June, 1895.

2. Notes on the Chaetognaths. Johns Hopkins University Circulars, No. 126, June, 1896.

3. The Inhibitory and Accelerator Nerves to the Crab's Heart (*an abstract*), by F. S. Conant and H. L. Clark. Johns Hopkins University Circulars, No. 126, June, 1896.

4. On the Accelerator and Inhibitory Nerves to the Crab's Heart, by F. S. Conant and H. L. Clark. The Journal of Experimental Medicine, Vol. I, No. 2, 1896.

5. Notes on the Cubomedusæ (*an abstract*). Johns Hopkins University Circulars, No. 132, November, 1897.

6. The Cubomedusæ. (This was accepted in June, 1897, as his thesis for the degree of Doctor of Philosophy, and it is here printed.)

TABLE OF CONTENTS.

INTRODUCTION.

Jelly-fish offer to the lover of natural history an inexhaustible store of beauty and attractiveness. One who has studied them finds within him a ready echo to Haeckel's statement that when first he visited the seacoast and was introduced to the enchanted world of marine life, none of the forms that he then saw alive for the first time exercised so powerful an attraction upon him as the Medusæ. The writer counts it a rare stroke of fortune that he was led to the study of a portion of the group by the discovery of two new species of Cubomedusæ in Kingston Harbor, Jamaica, W. I., while he was with the Johns Hopkins Marine Laboratory in June of 1896.

The Cubomedusæ are of more than passing interest among jelly-fish, both because of their comparative rarity and because of the high degree of development attained by their nervous system. One fact alone suffices to attract at once the attention of the student of comparative morphology —that here among the lowly-organized Cœlenterates we find an animal with eyes composed of a cellular lens contained in a pigmented retinal cup, in its essentials analogous to the vertebrate structure. Perhaps this and other facts about the Cubomedusæ would be more generally known, had they not been to a certain extent hidden away in Claus's paper on Charybdea marsupialis ('78), which, while a record of careful and accurate work, is in many respects written and illustrated so obscurely that it is very doubtful whether one could arrive at a clear understanding of its meaning who was not pretty well acquainted with Charybdea beforehand.

Before Claus's paper was received at this laboratory, H. V. Wilson went over essentially the same ground upon a species of Chiropsalmus taken at Beaufort, N. C. When the article on Charybdea marsupialis appeared, however, the results were so similar that Wilson did not complete for publication the careful notes and drawings he had made.

Haeckel's treatment of the Cubomedusæ in his "System" ('79) in the Challenger Report ('81) is much more lucid than Claus's; but the extended scope of his work and the imperfect preservation of his material prevented a detailed investigation, and for a more complete and readily intelligible

account of the structure of the Cubomedusæ a larger number of figures is desirable.

In the foregoing facts lies whatever excuse is necessary for repeating in the present paper much that has already seen print in one form or another.

Part I: SYSTEMATIC.

It seems advisable first of all to establish the systematic position of the two newly found species, Charybdea Xaymacana and Tripedalia cystophora. Haeckel's classification, as given in his "System der Medusen," is an excellent one and will be followed in this case. One of the new species, however, will not classify under either of Haeckel's two families, so that for it a new family has been formed and named the Tripedalidæ. In showing the systematic position of the two new forms, an outline of Haeckel's classification will be given, so far as it concerns our species, together with the additions that have been made necessary.

Cubomedusæ (Haeckel, 1877).

Characteristics: Acraspeda with four perradial sensory clubs which contain an auditory club with endodermal otolith sac and one or several eyes. Four interradial tentacles or groups of tentacles. Stomach with four wide perradial rectangular pockets, which are separated by four long and narrow interradial septa, or cathammal plates. Gonads in four pairs, leaf-shaped, attached along one edge to the four interradial septa. They belong to the subumbrella, and are developed from the endoderm of the stomach pockets, so that they project freely into the spaces of the pockets.

Family I: Charybdea (Gegenbaur, 1856).

Cubomedusæ with four simple interradial tentacles; without marginal lobes in the velarium, but with eight marginal pockets; without pocket arms in the four stomach pockets.

Genus: *Charybdea.*

Charybdeidæ with four simple interradial tentacles with pedalia; with velarium suspended, with velar canals and four perradial frenula. Stomach flat and low, without broad suspensoria. Four horizontal groups of gastric filaments, simple or double, tuft or brush-shaped, limited to the interradial corners of the stomach.

Species: *Charybdea Xaymacana* (Fig. 1).

Bell a four-sided pyramid with the corners more rounded than angular, yet not so rounded as to make the umbrella bell-shaped. The sides of the pyramid parallel in the lower two-thirds of the bell, in the upper third curving inward to form the truncation; near the top a slight horizontal constriction. Stomach flat and shallow. Proboscis with four oral lobes, hanging down in bell cavity a distance of between one-third and one-half the height of bell; very sensitive and contractile, so that it can be inverted into the stomach. The four phacelli epaulette-shaped, springing from a single stalk. Distance of the sensory clubs from the bell margin one-seventh or one-eighth the height of bell. Velarium in breadth about one-seventh the diameter of the bell at its margin. Four velar canals in each quadrant; each canal forked at the ends, at times with more than two branches. Pedalia flat, scalpel-shaped, between one-third and one-half as long as the height of bell. The four tentacles, when extended, at least eight times longer than the bell. Sexes separate. Height of bell, 18–23 mm.; breadth, about 15 mm. (individuals with mature reproductive elements); without pigment. Found at Port Henderson, Kingston Harbor, Jamaica.

As may be seen from the above, C. Xaymacana differs only a little from the C. marsupialis of the Mediterranean. Claus mentions in the latter a more or less well defined asymmetry of the bell, which he connects with a supposed occasional attachment by the proboscis to algæ. In C. Xaymacana I never noticed but that the bell was perfectly symmetrical. C. Xaymacana is about two-thirds the size given by Claus for his examples of C. marsupialis, which were not then sexually mature. It has 16 velar canals instead of 24 (32), as given by Haeckel, or 24 as figured by Claus. Difference in size and in number of velar canals are essentially the characteristics upon which Haeckel founded his Challenger species, C. Murrayana.

Family II: Chirodropidæ (Haeckel, 1877).

Cubomedusæ with four interradial groups of tentacles; with sixteen marginal pockets in the marginal lobes of the velarium, and with eight pocket arms, belonging to the exumbrella, in the four stomach pockets.

This family is represented in American waters by a species of Chiropsalmus, identified by H. V. Wilson as C. quadrumanus, found at Beaufort, North Carolina.

Family III: Tripedalidæ (1897).

Cubomedusæ with four interradial groups of tentacles, each group having three tentacles carried by three distinct pedalia; without marginal lobes in the velarium; with sixteen marginal pockets; without pocket arms in the stomach pockets.

Genus: *Tripedalia.*

For the present the characteristics of family and genus must necessarily be for the most part the same. The genus is distinguished by having twelve tentacles in four interradial groups of three each; velarium suspended by four perradial frenula; canals in the velarium; stomach projecting somewhat convexly into the bell cavity, with relatively well-developed suspensoria; four horizontal groups of gastric filaments, each group brush-shaped, limited to the interradial corners of the stomach.

Species: *Tripedalia cystophora* (Fig. 17).

Shape of bell almost exactly that of a cube with rounded edges; the roof but little arched. The horizontal constriction commonly seen near the top of the bell in the Cubomedusæ not present. Proboscis with four oral lobes; hanging down in the bell cavity generally more than half the depth of the cavity and at times even to the bell margin. In the gelatine of the proboscis an irregular number (15–21) of sensory organs resembling otocysts, from the presence of which comes the specific name. Phacelli brush-shaped, composed of from seven to thirteen filaments springing from a single stalk in each quadrant, or rarely from two separate stalks in one of the quadrants. Distance of the sensory clubs from the bell margin about one-fifth or one-fourth of the height of bell. Breadth of velarium about one-sixth the diameter of bell at margin; with six velar canals in each quadrant; the canals simple, unforked. Pedalia flattened, shaped like a slender knife blade, about half as long as the height of the bell. Tentacles at greatest extension observed two and a half times the length of pedalia. Sexes separate. Height of bell in largest specimens (reproductive elements mature) eight or nine mm. Breadth same as height or even greater. Color a light yellowish brown, due in large part to eggs or embryos in the stomach pockets. The reproductive organs especially prominent by reason of their similar color. Found in Kingston Harbor, Jamaica.

It will be seen from the above that Tripedalia possesses two of the

characteristics of the Charybdeidæ and two of the Chirodropidæ. The family was named from the prominent feature of the arrangement of the tentacles, in groups of three with separate pedalia. The small size of T. cystophora is worthy of note in connection with the fact that of the twenty species of Cubomedusæ given by Haeckel in his "System" only two are smaller than 20 mm. in height, and those are the two representatives of Haeckel's genus Procharagma, the prototype form of the Cubomedusæ, without pedalia and without velarium. While Tripedalia has both pedalia and velarium, it may be perhaps that its small size, taken in connection with characteristics just about midway between the Charybdeidæ and the Chirodropidæ, indicate that it is not a recently acquired form of the Cubomedusæ.

Part II: General Description of the Anatomy of the Cubomedusæ.

A: Charybdea Xaymacana.

a. *Environment and habit of life.*

1. The Cubomedusæ are generally believed to be inhabitants of deep water which come to the surface only occasionally. Both of the Jamaica species, however, were found at the surface of shallow water near the shore, and only under these circumstances. Whether these were their natural conditions, or whether the two forms were driven by some chance from the deep ocean into the Harbor and there found their surroundings secondarily congenial, so to speak, can be a matter of conjecture only. C. Xaymacana was taken regularly a few yards off-shore from a strip of sandy beach not ten minutes row from the laboratory at Port Henderson. It was seen only in the morning before the sea-breeze came in to roughen the water and to turn the region of its placid feeding-ground into a dangerous lee-shore. Some of the specimens taken contained in the stomach small fish so disproportionately large in comparison with the stomach that they lay coiled up, head overlapping tail. The name Charybdea, then, from the Greek χαρύβδις (a gulf, rapacious), seems to be no misnomer. It is worth mentioning that the digestive juices left the nervous system of the fish intact, so that from the stomach of a Charybdea could be obtained beautiful dissections, or rather macerations, of the brain, cord, and lateral nerves of a small fish.

In size C. Xaymacana agrees very well with the average of the genus. The four single tentacles characteristic of the genus are very contractile, varying from two or three to six or seven inches in length, and probably if measurements could be taken while the animal was swimming freely about, the length would be found to be greater still. Charybdea is a strong and active swimmer, and presents a very beautiful appearance in its movements through the water, the quick, vigorous pulsations contrasting sharply with the sluggish contractions seen in most Scyphomedusæ. With its tentacles streaming gracefully behind, an actively swimming Charybdea presents a fanciful resemblance to a

comet or meteor. When an attempt is made to capture one, it will often escape by going down into deeper water—as indeed do other jelly-fish. Escape from observation is all the more easy by reason of the entire absence of pigment excepting for the small amount in the sensory clubs. The yellowish or brownish color usually stated as common in the Cubomedusæ is nowhere present in C. Xaymacana.

b. *External Anatomy.*

2. *Form of Bell.* C. Xaymacana shows the typical division of the external surface into four almost vertical perradial areas (Figs. 1–3, *p*), separated by four stoutly arched interradial ribs or bands (Figs. 1–3, *i*). These ribs thus play the part of corners to the Cubomedusan pyramid. They are formed by the thickenings of the jelly of the exumbrella, and serve to give the necessary strength to the four interradial corners, each of which bears one of the four tentacles at its base. Each rib is further divided into two longitudinal strips by a vertical furrow lying exactly in the interradius (Fig. 2, *ifr*). The surface of the exumbrella is thus marked by twelve longitudinal furrows, as seen in the same figure (2). Of these, four are the interradial furrows just mentioned; the other eight are the adradial (*afr*) furrows, which set off the four perradial surfaces of the pyramid from the four interradial ribs or bands of the corners, each of which is again subdivided, as mentioned above, by the shallower interradial furrows. Each interradial furrow ends above the base of the corresponding pedalium, at about the level of the sensory club; each adradial furrow diverges toward the perradius in the lower third of its course, and thus with its companion furrow narrows down the perradial surface of the pyramid in the lower part of the bell to an area of not much greater width than the niches in which the sensory clubs lie. The projecting interradial corners are of course correspondingly enlarged in the lower part of the bell, and in this way the contours of the surface are changed from those figured in the view of the bell from above (Fig. 2) to those of Fig. 3, which represents a view of the bell margin from below.

3. *Pedalia.* From the base of the interradial corner bands spring the four pedalia (Fig. 1, *pe*), gelatinous appendages of the margin having much the same shape as the blade of a scalpel. These in turn bear on their distal ends, as direct continuations, the long, contractile, simple tentacles. The relatively stiff pedalia have the same relation to the flexible tentacles that a driver's whip-stock has to the long lash. In the living animal the pedalia are found attached to the margin at an angle

of about 45° with the longitudinal axis of the bell. In the preserved specimens they are bent in toward the axis by the contraction of the strong muscles at their base, in which position they are figured by Claus for C. marsupialis ('78, Taf. I., Figs. 1 and 2).

The pedalia are in reality processes belonging to the *subumbrella*, as will be shown in the section treating of the vascular lamella. They are composed chiefly of gelatine covered with thin surface epithelium and carrying within the gelatine the basal portion of the tentacle canals. They have received various names at the hands of the writers. Gegenbaur called them "Randblätter." Claus gave them the name of "Schirmlappen," and incorrectly homologized them with the marginal lobes of other Acraspeda. Claus's error was corrected by Haeckel, who termed them "Pedalia" or "Gallertsockel," and homologized them with the pedalia of the Peromedusæ. Besides furnishing a base of support for the tentacles they may perhaps also serve as steering apparatus, a function for which their thin blade-like form would be admirably adapted.

Internal to the base of each pedalium, between it and the velarium, is found a funnel-shaped depression of the ectodermal surface. This is shown in Fig. 5 (*ft*) in longitudinal section, and in cross-section in Fig. 16. In the latter figure the epithelium of the outer wall of the funnel (*mt*) is shown much thickened, the result of a stout development of muscle fibres. These are the muscles that in the preserved specimens cause the inward contraction of the pedalia referred to above.

4. *Sensory Clubs* (marginal bodies, rhopalia). In spite of their position above the bell margin, the four sensory clubs, representing as they do transformations of the four perradial tentacles, are properly classed with the pedalia and interradial tentacles as appendages of the margin. They lie protected in somewhat heart-shaped excavations or niches in the perradial areas of the exumbrella. Each sensory niche is partially roofed over by a covering scale, a hood-like projection from the exumbrella. Below the covering scale the water has free access to the niche and to the sensory club within it. The sensory club consists of a hollow stock directly homologous with tentacle and canal, and a terminal, knob-like swelling, the sensory portion proper. The latter contains on its inner surface—the surface turned towards the bell cavity—two complicated unpaired eyes with lens, retina, and pigment, lying one above the other in the median line; and at the sides of these, two pairs of small, simple, pigmented, bilaterally symmetrical eye spots. At the end of the club, that is, on its lowermost point, lies a sac that contains a

concretion and is usually considered auditory. The canal of the stalk is directly continuous with the gastro-vascular system. In the swollen knob of the sensory club it forms an ampulla-like terminal expansion.

As was pointed out by Claus, the bottom of the sensory niche—by bottom is meant the vertical wall that separates the space of the niche from the bell cavity—is formed from the subumbrella only. This arrangement of parts, apparently impossible for a structure so far removed from the bell margin as the sensory niche, will be explained more fully under the special topic of the vascular lamellæ, or cathammal plates. It is sufficient at this point to refer to Fig. 44, which shows the shield-shaped area mapped out by a vascular lamella that connects the endoderm of the stomach pocket with the ectoderm of the bottom of the niche. By this the exumbrella is completely cut off from any part in the formation of the bottom of the niche. Cross and vertical sections through the niche (Figs. 39 and 37) help to a better understanding of these relations. Since the base of the stalk of the sensory niche lies within the ring of vascular lamella, the whole organ as well as the bottom of the niche belongs to the subumbrella, and so in spite of its position some distance upwards from the bell margin the sensory club is very properly called a "marginal body" (Randkörper).

The epithelium of the sensory niche consists entirely of the flattened ectodermal surface layer common to the whole exumbrella. No differentiation suggestive of nervous function in addition to that of the sensory clubs can be discovered, although it would be quite natural to expect to find something of the sort, as intimated by Claus ('78, p. 27).

It is worth while to mention again the fact that the eyes are directed inwardly toward the cavity of the bell. The larger and lower of the two median eyes looks into the bell cavity horizontally; the smaller upper eye is turned upward toward the region of the proboscis. This is in the normal pendant position of the sensory club. The stalk, however, is very flexible, and a range of other positions of the sense organs is possible, although nothing was observed to suggest that such positions were within the control of the animal. The eyes evidently have as their chief function to receive impressions of what is going on *inside* the bell, not outside. Perhaps the strongly biconvex, almost spherical lenses of the median eyes also point to a focus on near and small objects.

5. *The Bell Cavity and its Structures.* In general, the bell cavity repeats the external form of the bell, being almost cubical. In cross-section it appears very nearly square with the angles in the interradii as

seen in the series of drawings that figure sections of the whole jelly-fish at different levels (Figs. 6–16). Above, the bell cavity is roofed over by the stomach; below, it is open freely to the water, the opening being narrowed somewhat by the diaphragm-like velarium (Fig. 3, *v*); the four flat perradial sides are bounded by the walls of the four broad stomach pockets, to be described when we come to the internal anatomy.

(a) *The Proboscis.* From the stomach there hangs down into the bell cavity the proboscis or manubrium, which consists of a short funnel-shaped stalk bearing on its distal end the four mouth lobes or lips. The latter are somewhat broadly V-shaped processes lying in the perradii with the convexity directed outwards, and with the concavity on the inside forming the beginnings of four perradial furrows that are continued upwards to the stomach. The four furrows are shown in the stalk of the proboscis in Fig. 11, which represents a section taken a little above the level of the mouth lobes. The same cross-shaped section of the stalk shows the four perradial prominences or ridges overlying the furrows, which are the direct continuations of the four projecting mouth lobes.

(b) *The Suspensoria or Mesogonia.* The stomach (leaving out of consideration the proboscis) hangs down into the bell cavity as a slightly sagging saucer-shaped roof (Figs. 4 and 5). In the four perradii it is attached to the lateral walls of the subumbrella by four slenderly developed mesentery-like structures, the suspensoria or mesogonia. These are simple ridges of gelatine, covered of course with the epithelium of the bell cavity, which serve to keep the stomach in position much in the way that a shelf is supported by brackets (Fig. 4, *su*). The suspensorium accordingly has two parts, curved so as to lie at right angles with each other: a vertical portion lying along the wall of the subumbrella, and a horizontal which passes over from the vertical on to the basal wall of the stomach. In Fig. 10 the suspensorium in each quadrant is shown cut across just below the angle between the two parts, so that the two appear in the section as projections on the wall of the stomach and on the wall of the subumbrella.

(c) *The Interradial Funnels or Funnel Cavities.* It will be seen at once that the four suspensoria serve as partitions to divide the upper portion of the bell cavity, the part that lies between the stomach and the lateral walls of the subumbrella, into four compartments. These compartments extend upwards in the four interradii like inverted funnels, whence their name. In the series of cross-sections they can be traced

upwards with constantly diminishing area from the level of the suspensoria, Fig. 10 (*i f*), to Fig. 6, which is taken very near the top of the bell. Homologous structures exist in all the Scyphomedusæ, and in some of the Lucernaridæ they are continued up even into the stalk of the attached jelly-fish.

(d) *The Velarium.* Charybdea, like most of the Cubomedusæ, possesses a velum-like structure around the opening of the bell cavity (Fig. 3, *v*). The velarium is a thin muscular diaphragm, resembling the true velum in position and essential structures, but differing from the velum in its origin, and in the possession of diverticula from the gastrovascular system, the velar canals. Of these there are in C. Xaymacana very regularly sixteen, four in each quadrant. Their outline is seen in Fig. 3 to be forked with small irregular accessory processes. As for its origin, the velarium of the Cubomedusæ is commonly accounted to have arisen by fusion of marginal lobes, as in the case of the velarium of the Discomedusæ. Pending decisive ontological evidence, the slight notches in the four perradii seen in Fig. 3 may perhaps be taken as slight indications of a primitive unfused condition, but the question will be brought up again when the vascular lamellæ are discussed.

(e) *The Frenula.* Just as the stomach is attached to the walls of the subumbrella in the four perradii by the suspensoria, so in the lower part of the bell cavity the velarium is attached to the wall of the subumbrella in the perradii by four structures similar to the suspensoria, the frenula velarii. The frenula, like the suspensoria, resemble the brackets of a shelf, with the difference that in the case of the frenula the bracket is above the shelf, their purpose being evidently to keep the velarium stiff against the outflow of water produced by the pulsations of the bell. According to the greater need of strength in this case, we find the frenula stouter, more buttress-like than the suspensoria. The gelatinous ridge that gives them the necessary firmness is thickened so as to be triangular in section, as shown in Fig. 16 (*frn*).

(f) *Musculature.* As is general in medusæ, the muscular system, so far as known, is restricted to the subumbrella. It has a very simple arrangement, consisting of a continuous sheet of circular (*i. e.* horizontal) striated fibres, which is interrupted only in the four perradii by the radially directed muscle fibres of the suspensoria and the frenula. In each quadrant, between the muscle of the suspensorium above and that of the frenulum below, in an area just internal to the sensory niche, there lies a space free from muscle. This interruption of the muscle

layer is shown in Fig. 39. Under the head of musculature belonging to the subumbrella must be included also the radial, or longitudinal muscles at the bases of the pedalia, which were mentioned before (Fig. 16, *mt*). The mouth lobes and proboscis also are highly contractile and muscular.

(g) *Nerve Ring.* It is in the possession of a clearly defined nerve ring that the Cubomedusæ differ from all other Scyphomedusæ whose nervous system has been carefully studied. The nerve ring shows very plainly on the surface of the subumbrella as a well-defined clear streak. Its course is zig-zag or festoon-like. In the interradii, at the basis of the tentacles, it lies not far from the bell margin. In the perradii it rises to the level of the sensory clubs. This very striking arrangement is understood at once when it is remembered that the sensory clubs represent the four perradial primary tentacles, and were originally situated on the margin. When all the rest of the margin grew down and away from the four sensory clubs, fusing below them to form the present intact edge of the bell, the four portions of the nerve ring that lay in the perradii were left at the level of the sensory clubs, and the originally straight nerve ring was thus bent into a bow in each quadrant. The finer structure of the nerve will be treated of in the special part to be devoted to the nervous system.

c. *Internal Anatomy.*

6. *Stomach.* The shape of the stomach is approximately that of a biconvex lens, as seen in Fig. 4, which represents a Charybdea cut in halves longitudinally in the perradius. The lumen of the proboscis (the buccal stomach according to Haeckel's terminology) communicates directly by a funnel-shaped enlargement with the stomach proper, or central stomach of Haeckel. The term basal stomach is carried over by Haeckel from the Stauromedusæ, where it has considerable significance, to the Cubomedusæ, and applied to the upper part of the central stomach. In the stalkless Cubomedusæ, however, it has no significance so far as actual structure goes, and our knowledge of the development of the Cubomedusæ is as yet too simple for us to say that the upper part of the main stomach represents what remains of the basal stomach of an earlier pedunculated stage.

The epithelium of the roof of the stomach is not specially differentiated and apparently has little or no part in digestion. The epithelium of the floor, on the other hand, is composed chiefly of very high and thickly crowded columnar cells which are usually described as coarsely granular,

but under high powers appear to be filled with vacuoles surrounded by a network of cell substance. Thickly interspersed among these columnar cells are goblet cells filled with mucus. The floor is thrown into numerous wrinkles by ridges in the supporting gelatine resulting in increase of digestive surface. The four perradial grooves of the proboscis are continued in the perradii along the floor of the stomach as four fairly deep furrows, which lead directly to the gastric ostia and stomach pockets—structures to be described presently. These furrows are lined with crowded columnar cells, smaller and denser than the other cells of the digestive epithelium, containing no granules and but little beside the relatively large, compact, deeply staining nuclei. The furrows probably represent special ciliated courses.

7. *Phacelli.* Lying in the four interradial corners of the stomach are the four phacelli or tufts of gastral filaments to the number of thirty or thirty-five in each tuft. The filaments are attached to a single stalk, like the fringe of an epaulette or the hairs of a coarse brush. The stalk bearing the filaments is an outgrowth of the lower wall of the stomach just at the point where it fuses with the upper. The phacelli are therefore structures of the subumbrella, proof of which will be found under the special topic of the vascular lamellæ. The stalk, an indication of which appears in *sph.* Fig. 6 (the section being a little below the axis of the stalk, which lies horizontally), consists of a firm core of gelatine covered with the high columnar epithelium of the floor of the stomach. The filaments themselves are slender processes repeating the structure of the stalk and having a central axis of gelatine for support covered with glandular epithelium, which in the case of the filaments bears numerous nettle cells. These processes are extremely contractile, and in the living animal show a continuous, slow, squirming movement like a mass of worms. The section just referred to (Fig. 6) shows diagrammatically three of these filaments (*fph*) cut across in each quadrant.

8. *Peripheral Part of the Gastro-vascular System.* The proboscis and stomach proper comprise the central part of the gastro-vascular system. In direct communication with the central is a peripheral part composed of pouches or pockets lying in the vertical sides of the cube-shaped bell, just as the central stomach lies in its roof. The peripheral part may be subdivided for convenience of description into the stomach pockets, the marginal pockets, and the canals of the tentacles and sensory clubs.

(a) *Stomach Pockets.* These are four broad, thin pouches lying between the exumbrella and the subumbrella in the four perradii (*e. g.*

Fig. 9, *sp*) and separated from one another in the interradii merely by four thin vertical strips of vascular lamella (*ivl*) or fusion between the two endodermal surfaces of a primitively single undivided peripheral cavity. The structure is exactly that which we should have if in a Hydromedusa, for example Liriope (Trachomedusæ), the four radial canals broadened out and the intervening cathammal plates correspondingly narrowed, until the relations in size were just reversed, and instead of four narrow radial canals separated from one another by four broad cathammal plates, we had four broad radial canals or pouches separated by four narrow cathammal plates.

The stomach pockets communicate at their top with the central stomach by means of four moderately large openings, the gastric ostia. These are seen in a side view of the whole animal as triangular spaces (Fig. 1, *g. o.*) near the top of the broad perradial sides. In Figures 7 and 8 they are seen in cross-sections, in Fig. 4 in vertical section.

The communication between the stomach and each stomach pocket is guarded by a valve that can cut the one entirely off from the other. The valve is simply the flexible lower margin of the gastric ostium, a thin vertical fold of the floor of the stomach, semilunar in shape, just at the point where it is passing over into the stomach pocket. A longitudinal section, such as is shown in Fig. 4, gives the best idea of the form and position of the valve that can be obtained from any simple section. Internal to the valve is seen a depression of the stomach wall, almost worthy to be called a pocket. The valve itself lies as a wall across the end of this depression, obstructing a free course to the stomach pocket. It will be seen at once that any pressure of fluids in the stomach against this vertical wall, or valve, would serve only to press it against the inner surface of the exumbrella, and thus effectually close the entrance into the stomach pocket. Such a closure would both keep the juices of the stomach from entering the pockets and the embryos in the pockets from entering the stomach before the proper time.

The depression of the floor of the stomach just internal to the valve may possibly be a structure of some morphological significance. In one series of sections it was found that in two of the quadrants the depression was deeper than that represented in Fig. 4, and extended perceptibly into the outer or vertical portion of the suspensorium. Fig. 32 is a diagram giving a vertical reconstruction in the perradius of the cross-sections in which this deepened depression was noticed. Fig. 31 is a drawing (the outline by camera lucida) of one of the cross-sections, through the lower-

most point of the depression. The figure gives the wall of the stomach lined with high columnar epithelium (*ens*), and the wall of the stomach pockets, with the suspensorium (*su*) connecting them. The section is taken just above the broad angle that lies between the two parts of the suspensorium, that is, in a plane parallel to the arrow *a–b* in Fig. 32, but a little lower down. At the points to which the reference letter *x* (Fig. 31) refers are seen the first indications of the division into two parts, *i. e.* of the apex of the angle. The next section or two lower down show the relation seen in Fig. 10 (*su*). There can be no doubt in this case that the depression or pocket lies in the outer vertical limb of the suspensorium. It is the position that gives it at least the appearance of some morphological significance. In two genera of Lucernaridæ named and described by Clark ('78), Halicyathus and Craterolophus, the mesogonia or suspensoria in all four perradii contain broad pockets. These mesogonial pockets in the Lucernaridæ have given rise to considerable misunderstanding owing to the fact that in some forms the reproductive organs bulge out from the stomach pockets in which they structurally lie, and come to take up a secondary position in the walls of the mesogonial pockets. The sections of Charybdea above referred to indicate that among the Cubomedusæ we may have the same structure reduced to its lowest terms, and may be a feather's weight in favor of the view that the Cubomedusæ are descendants of an attached Lucernaria-like form.

Two more diagrams, Figs. 33 and 34, are added in order to give a more complete understanding of a gastric ostium and its neighboring structures, the mesogonial pocket and the valve. Fig. 33 is a view of the gastric ostium and valve from the stomach side, and represents the appearance that would be given by a thick section through the arrow *x–y* in Fig. 32, in a plane at right angles to the paper. The heavy lines outlining the gastric ostium (*em* and *enfl*) represent the place where the plane of the section has cut across the epithelium of the roof of the stomach above the ostium and the epithelium of the floor of the pocket-like depression internal to the valve. The continuation of the two heavy lines in either side of the ostium represents the region where the roof and floor of the stomach meet; *i. e.*, the edge of the lens-shaped stomach. The semilunar outline of the valve (*vg*) is shown by a light line just above the epithelium of the depression. As is seen by the reference arrow in Fig. 32, the valve lies a little external to the immediate plane of the section, and hence it is that its inner surface is seen in Fig. 33 and not a section of it. The vertical part of the suspensorium (*su*) is seen in section below the epithe-

lium of the depression. The reference numbers 1, 2, 3 and 4 denote the same points in Figs. 32 and 33. Fig. 32 referred to Fig. 33 would lie in a plane at right angles to the paper through the reference arrow *x–v* of the latter figure.

Fig. 34 represents a horizontal section through the gastric ostium at the level of the arrow *a–b* in Fig. 32, or arrow *c–d* in Fig. 33. The reference numbers 5, 6 and 7, 8 denote similar points in the two figures 33 and 34. Fig. 32 as referred to Fig. 34 is through the arrow *e–f*; Fig. 33 is through the arrow *c–d*. In the series of cross-sections, Fig. 9 is taken at a level a little below that of Fig. 34, and passes through the basal part of the valve (*vg*).

(b) *Marginal Pockets.* The part of the peripheral portion of the gastro-vascular system in each quadrant which is called the stomach pocket extends downwards as far as the sensory niche. Here by the coming together of the walls of the exumbrella and subumbrella the space between them is obliterated (Fig. 15) in the immediate perradius. From the sensory niche downward to the margin each stomach pocket is thus divided into two smaller pouches, the marginal pockets (*mp*). In each side of the Cubomedusan cube there are, then, in Charybdea two marginal pockets; or in all eight, a characteristic of the family Charybdeidæ. The marginal pockets as the name implies extend downwards to the bell margin, and are continued into the velarium as the velar canals. Of these (Fig. 3) there are two from each marginal pocket, or sixteen in all. The constancy in their number is one of the characteristics that distinguish C. Xaymacana from the very closely related C. marsupialis of the Mediterranean. (Compare Fig. 3 with the similar one by Claus for C. marsupialis, '78, Taf. I., Fig. 6.) The forked shape, while to be sure the common form in C. marsupialis, is an almost invariable characteristic in C. Xaymacana. It may be mentioned again that the presence of these canals is one of the chief features that distinguish the velarium of the Scyphomedusæ from the velum of the Hydromedusæ.

(c) *Canals of the Sensory Clubs and Tentacles.* The four interradial definitive tentacles and the four perradial transformed tentacles, the sensory clubs, are hollow, and their canals communicate directly with the peripheral part of the gastro-vascular system. The canal of the sensory club in each quadrant leads directly out from the stomach by a somewhat funnel-shaped opening formed by the approximation of the two walls of the stomach pocket. The relation of the canal of the sensory club to the stomach pocket is seen at a glance in Fig. 37. It is given by means of cross-sections in Figs. 12–14. Figure 12 shows the inner

walls of the stomach pocket approaching the outer at two points, leaving between them a concavity freely open to the rest of the stomach pocket above and at the sides. Fig. 13, a little lower down, shows the two walls fused together at two points, making the interspaces a definite canal communicating with the stomach pocket above only. This canal lies directly over the sensory niche, and in the next figure (No. 14) the canal is seen to have passed through the roof of the sensory niche and to have entered the base of the stalk of the sensory club. In the enlarged end of the club, the part which bears the sensory structure, the canal widens into a terminal ampulla-like sac.

The endoderm lining the canal of the sensory club is specially differentiated. In the stalk it is more columnar than the epithelium of the stomach pockets, and is made up of cells containing a brightly staining nucleus with very little trace of cytoplasm. The cell bodies appear as if filled with a clear, non-staining fluid. Perhaps these cells give the stalk elasticity to act in connection with the thin layer of longitudinal muscle-fibres that are found just external to the supporting lamella. The epithelium of the terminal enlargement of the canal is composed of very high narrow cells, many of which show two nuclei of equal size and staining quality lying side by side.

In continuation of the specialized epithelium of the perradial furrows in the floor of the stomach the inner wall of the stomach pocket shows a strip of similar densely crowded columnar cells leading from the gastric ostium downwards to the canal of the sensory club. As in the other case, the strip probably represents a specially ciliated tract, and perhaps in it we see the reason why the canal of the sensory club is almost always found to contain either spermatozoa which are shed by the male reproductive organs directly into the stomach pocket, or else floating cells of the kind to be described in the next section.

The canals of the interradial tentacles arise from the peripheral gastro-vascular system much lower down than those of the sensory clubs, since these tentacles have preserved their primary positions with reference to the bell margin. Figure 16 represents a section taken at the level of the base of the pedalia which gives the connection of the tentacle canals with the gastro-vascular system. At the level below the sensory niche the four broad stomach pockets have been divided, as we have seen, into the right marginal pockets (*mp*). The figure shows that in the interradial corners the longitudinal septa (*ivl*, in the preceding figures), or lines of fusion between the two walls of the peripheral gastro-vascular

space, which divide the primitively simple space into the four stomach pockets, have come to an end, leaving a connecting canal (*cc*) in each corner as all that remains of the primitive uninterrupted communication between all parts of the peripheral system. It is from these four connecting canals that the tentacle canals take their origin. From this point of origin each tentacle canal passes downwards, surrounded by the gelatine of the pedalium, into the tentacle proper.

The connecting canals are of morphological importance in that they are supposed, with much reason, to represent in the Cubomedusæ the circular canal of the Hydromedusæ.

9. *Reproductive Organs.* The sexes are séparate in Charybdea. In both sexes the reproductive organs consist of four pairs of long leaf-like bodies, each leaf attached along one edge to the wall of the subumbrella in an interradius (see Fig. 1, *r*), and hanging free in the stomach pockets. From this position in the stomach pockets it is evident that the reproductive organs are endodermal. The lines of attachment of each pair is just internal to the longitudinal vascular lamella that fuses the outer and inner walls of the stomach pockets together in the interradius (*ivl*), and the reproductive organs are therefore structures belonging to the subumbrella. It is interesting to note how careful examination of the medusan organization takes away from the importance of the outer cup, the exumbrella, and adds to that of the inner, the subumbrella. We have seen that the phacelli and the sensory clubs, from whose position it would be supposed, that they belonged to the exumbrella, are organs of the subumbrella, and that there is no muscle-tissue in the exumbrella; we find now that the reproductive organs belong to the subumbrella, and it will be shown later that the tentacles, like the sensory clubs, are structures of the subumbrella also. To the exumbrella are left only the functions of support and covering.

The mature reproductive organs extend very nearly throughout the entire vertical length of the bell, and are therefore found in the series of cross-sections in all but the uppermost and lowermost (Figs. 7–15 *r*). The organs consist of germ cells within, covered by an epithelium of columnar cells that shows here and there nettle cells. The ova are found with different amounts of yolk, according to age, surrounding a large nucleus almost devoid of chromatin and an intensely staining nucleolus. In young ova there appears very plainly in every case at least one small deeply staining body inside the nucleus, which very much resembles the nucleolus. These are probably so-called yolk nuclei, and while I have not

made a special study of the ovogenesis, I infer that the constant presence of at least one, points to an origin of the ovum from a syncytium (of at any rate two cells), similar to that which has been recently shown by Doflein ('96) to occur in the formation of eggs in Tubularia. In the nearly mature ovary each ovum is surrounded by a layer of gelatine, which comes from the gelatinous sheet that enters the leaf-like ovary for its support along its line of attachment just internally to the interradial septum. It seems as if the ova, arising in the epithelium on the surface, pushed their way into the gelatine inside and there completed their development entirely surrounded by a slight investment of gelatine, which grows thinner around each ovum as it increases in size. In males the testes always show a similar division into compartments by gelatinous meshes, the compartments thus mapped out being filled with the small brightly staining spermatocytes. Ova and spermatozoa when mature are set free in the stomach pockets.

10. *Floating and Wandering Cells.* In the stomach pockets, the canals of the sensory clubs, and even in the stomach itself, are found in varying numbers freely floating cells having the appearance of young ova. They vary in size, the smallest being of the size and having the general aspect of the small ovocytes found in the ovary. The largest (Fig. 70) have exactly the same structure as the young ovarian eggs before they have begun to accumulate yolk. The granular deeply staining cytoplasm, the clear non-staining nucleus with its bright nucleolus and the nucleolus-like yolk nucleus, all show beyond doubt that these freely floating cells originate in the ovary.

In some of my preparations these cells are found not only floating free, but wandering through the tissues. Fig. 70 shows two such wandering cells fixed just as they were making their way either through the digestive epithelium into the gelatine of the floor of the stomach, or from the gelatine into the epithelium. The former seems the more probable, though why they should want to get into the gelatine is not very easy to conceive.

Perhaps there is some connection between this and the appearance that the young ovarian eggs have of pushing their way from the epithelium into the gelatine of the ovary. And of course it is not impossible that the whole phenomenon is abnormal, due to rupture of the ovaries which sets free young ova to exhibit their amœboid tendencies under new conditions. Against such an explanation, on the other hand, might be urged the fact that what seem to be the small floating cells are found

occasionally in males as well as females, and that in the females a series can be traced with a good degree of certainty between the small floating cells like those found in the walls, and the larger ones which have all the characteristics of young ova.

However that may be, this amœboid action of cells having the structure of ova brings to mind the remarkable form of asexual reproduction described by Metschnikoff for Cunina proboscidea, under the name of "Sporogonie." Unfortunately Metschnikoff's original paper was not accessible to me, so that I was unable to obtain more particulars on the subject than those given in Korschelt and Heider's text-book (p. 33). The reproductive organs of both males and females of Cunina proboscidea are said to produce, besides the usual distinctively sexual elements, neutral amœboid germ cells, which wander into the endoderm of the stomach and circular canal, and also penetrate into the gelatine of the subumbrella. These amœboid cells divide parthenogenetically. One of the two cells of the first cleavage continues to divide and eventually forms an embryo of Cunina; the other remains amœboid and serves for movement, attachment and nourishment of the embryo.

Charybdea, however, has shown no sign of any such reproductive process on the part of its floating and wandering cells. The only indication that I get as to their use points to a possible nutritive function. The enlarged terminal portion of the canal of the sensory club almost invariably contains a number of the small-sized floating cells. These have a vacuolated, half disintegrated appearance, with the nucleus always compact and brightly staining. Now, examination of the high columnar cells that line the enlargement of the canal shows the presence in the cells of bodies of exactly the same appearance as those in the lumen. In one case a floating cell was found just at the end of an epithelial cell, to all appearance half ingested. The identity of the bodies inside the cells and those in the lumen is shown very clearly in some sections of material fixed in formalin, which preserves nuclei, cell walls and general outlines well enough, but does not retain the cytoplasm, and hence is useless for most purposes of histology. In the endodermal cells of the terminal enlargement thus preserved are found all the more distinctly the bright, compact, degenerated nuclei of the ingested cells, while in the lumen are seen other bright, compact nuclei with the poorly preserved remains of cell substances around them. In addition to the evidence from the appearance of the floating cells themselves and their ingestion by the endodermal cells, a little collateral evidence may perhaps be brought in

from the Tripedalia about to be described. From the ovaries in this form are detached masses of cells (Fig. 71) which float free in the stomach pockets among the developing embryos, and to judge from the vacuolation that appears, are used up in their favor. These cell masses are described more fully in the part on Tripedalia.

B: Tripedalia cystophora.

a. *Habitat.*

The species upon which the new family was founded was obtained in great abundance in one locality in Kingston Harbor in the summer of 1896. The environment was even more unlike that in which Cubomedusæ have been found heretofore than in the case of Charybdea Xaymacana. On the west side of the Harbor there is a part more or less cut off from the main body of water, and so from the ocean, by a peninsula. This sheltered bay is dotted with small mangrove islands which toward the head of the bay become so numerous as virtually to convert it into a mangrove swamp. The water is shallow and discolored with organic matter, showing that the tide does not exercise much influence here, and the bottom is for the most part a black mud, deep enough to make wading very uncomfortable but not impossible near shore. The islands rise but slightly above the level of the waters, and the thick vegetation that covers them, for the most part mangroves, grows out into the water on all sides, forming a fringe of overhanging boughs. It was here in the shelter of the boughs, among the roots and half-submerged stems of the mangroves, that the small Cubomedusa was found to thrive. It could be obtained in great abundance almost any day, and of all sizes from the largest adults with stomach pockets filled with eggs or embryos down to small specimens only about two millimeters in diameter. In but one other place was Tripedalia found, and that was a similar region of half landlocked water skirted with mangroves, situated near Port Royal, across the harbor from the locality just mentioned. It would be hard to find places in which the conditions of life were more strikingly different from those of the pure deep sea in which the Cubomedusæ have been generally found before. The slight brownish yellow pigment made the small medusæ a little difficult to see in the discolored water, but like the pellucid Charybdea in the clear water of the harbor, their active movements gave away their presence. The swimming was very vigorous and was effected by quick, strong pulsations (as many as 120 per minute were counted), very different from the slow, rhythmic contractions of the

Discomedusan Cassiopea which was found in the same region over by Port Royal. Whether or not the animal made intentional efforts to escape capture could not be decided satisfactorily, but certain it was that they did escape often enough by swimming quickly below the surface of the semi-opaque water.

Tripedalia endured captivity much more hardily than the Charybdea, and would live in aquaria happily enough for a number of days—no attempt was made to see how long. Specimens with their stomach pockets filled with ripe spermatozoa, or with young at any stage from egg to planula, were taken in plenty from the latter part of June to the latter part of July. In each female the young were all at the same stage. The embryos were thrown out in the aquaria as free-swimming planulæ, which settled down on the bottom and sides of the glass in a day or two, and quickly developed into small hydras with mouth and typically with four tentacles (and four tænioles, W. K. B.), though three and five were by no means uncommon. In this condition they lived for three weeks without essential change, and they were still giving no promise of further development when the laboratory broke up and the jars had to be emptied.

b. *External Anatomy.*

The structure of the Cubomedusæ seems to be that of a type well established, and accordingly offers no very wide range of diversity among the different genera. The Charybdea that has just been described is a very typical form and will serve well as a standard with which to compare our species of Tripedalia. The resemblances are so close that a detailed account of the anatomy of the second form would involve much needless repetition. It is hardly necessary to do more than merely point out in what points Tripedalia resembles Carybdea and in what points it differs.

The form of the bell is less pyramidal than in Charybdea. Some measurements even gave the breadth greater than the height. The external surface is divided, as typical for the Cubomedusæ, into the four perradial sides and the four convex interradial ridges, and the furrows that separate these areas are with one small exception exactly the same as those of Charybdea, as may be seen by comparing the series of sections of Tripedalia (Figs. 21–30) with those of Charybdea (Figs. 6–15). The exception is almost too slight to mention. The adradial furrow in each octant which sets off the corner rib from the perradial surface in

the lower part of the bell is not directly continuous, as in Charybdea, with the corresponding furrow in the upper part of the bell—that is, the *afr'* of Figs. 24–27 is not continuous with the *afr* of Figs. 22 and 23, as is seen by both being shown in Fig. 24. The upper furrow (*afr*) is continued only a short distance, however, below the starting point of the lower (*afr'*).

The pedalia conform entirely to the description given those of Charybdea, except that there are three attached to the bell margin in each interradius instead of one, and that the blade of each pedalium is much narrower.

The sensory clubs also show exactly the same relation to the bell and exactly the same structure.

In the bell cavity the proboscis has a longer and better defined stalk than that of Charybdea, and has the further and more important difference of possessing special sensory organs, to the number of fifteen or twenty. The suspensoria are much more developed than in Charybdea, so that the interradial funnels lying between are more marked. In a corresponding way the frenula are larger and stouter (Figs. 28, 29, *frn*). The musculature shows no new features and differs only in being comparatively more strongly developed and having a more pronounced striation. The nerve ring follows the same looped course from the margin in each interradius up to the level of the sensory clubs in the perradius.

c. *Internal Anatomy.*

The stomach offers no peculiarities, and the phacelli also agree with those of Charybdea except in having a smaller number of filaments in each tuft. The stomach pockets are not guarded by such well-developed valves as those described for Charybdea, though the valvular nature of the lips of the gastric ostia is indicated and the valvular functions undoubtedly performed. The gastric ostia are smaller (cf. Figs. 7 and 22), and this makes highly developed valves less necessary. No trace of anything corresponding to mesogonial pockets was noticed.

In the matter of the marginal pockets, however, we find that the agreement with Charybdea is no longer continued. The regions that correspond to the eight marginal pockets of Charybdea are formed, as in that genus, by the coming together of the exumbrella and subumbrella at the sensory niche (Figs. 25–28), but each of these regions is subdivided, as it is not in Charybdea, into two marginal pockets, a larger (*mp*, Figs. 28–29) and a smaller (*mp'*). In this way sixteen marginal pockets are

formed as in the Chirodropidæ. Furthermore, as happens in the latter family but does not in the Charybdeidæ, the marginal pockets extend into the velarium. From each of the larger marginal pockets are given off two velar canals, while each of the smaller gives rise to but one short one (Fig. 18). Fig. 30 represents one of the last sections of a Tripedalia cut transversely, in which nothing but the pedalia and the velarium appear, and in it are shown the velar canals (*vc*), which come from the larger marginal pockets. The velarium appears in four segments because it is drawn upwards in the four perradii by the frenula (see Fig. 20). That the canals from the smaller pockets do not appear in the section is due to their shortness and to the fact that they are pulled upwards above the level of the sections by the frenula, together with that portion of the velarium.

The smaller velar canals, a pair in each perradius, seem to have in the males some function in connection with the storing of matured spermatozoa. In specimens with ripe testes they are very often found crowded to distension with spermatozoa, while the other velar canals may or may not contain them, and generally do not. The epithelium lining them is, like that of the others, composed of columnar cells higher on the wall turned toward the bell cavity than on that turned towards the exterior, but otherwise not specially differentiated. I searched in vain for any trace of opening by which the spermatozoa might gain the exterior. Fig. 29 shows another point which may be mentioned in passing, namely, that the canal of each of the three tentacles opens into the peripheral gastro-vascular system independently. The central tentacle of each group is the homologue of the single tentacle of Charybdea, and is formed in Tripedalia before the two lateral tentacles appear. Its communication with the peripheral pocket system is higher up than the openings of the lateral tentacles, so that in the section drawn the latter are just beginning to be indicated (*ct'*).

It remains only to speak of the reproductive organs of Tripedalia. The sexes are separate in this form also, and ovaries and testes have the same structure as is found in other Cubomedusæ. The development of floating masses of cells in the females, however, is a feature which, so far as I know, has not been observed before. These masses, of which a small one is represented in section by Fig. 71, are apparently developed along with the eggs, and repeat the structure of the ovary to all intents the same as if they were various-sized fragments of it broken loose. They consist mostly of high, columnar epithelial cells surrounding a few

central cells and showing here and there a nettle cell just as the reproductive organ does. The epithelial cells differ from those of the ovary in containing one or more large vacuoles, and this vacuolation increases as the embryos, among which the masses float, develop. The idea naturally suggests itself, therefore, that they serve for nourishing and perhaps for protecting the embryos while they are developing in the stomach pockets of the mother individual.

Part III: DESCRIPTION OF SPECIAL PARTS OF THE ANATOMY.

A: The Vascular Lamellæ.

In Medusæ it is a common thing to find that in certain definite places of the gastro-vascular system two endodermal surfaces that were primarily separated by a space have come together and fused into a single lamella or plate. Such a structure is called indifferently a cathammal plate, an endodermal lamella, or a vascular lamella. In the adult animal the vascular lamellæ are by virtue of their very nature formations "with a past." They are scaffolding left in the completed structure, giving us clues as to the way in which that structure was brought about; and in the Cubomedusæ, whose development is as yet unknown, they therefore afford an unusually interesting subject for special consideration.

The vascular lamellæ that are found in Charybdea and Tripedalia may for convenience be described as forming two systems, the internal and the marginal. The former comprises the endodermal fusions that separate the stomach from the stomach pockets (except for the spaces of communication left free, the gastric ostia) and those that separate the stomach pockets from one another. The marginal system consists of the lamella that connects *endoderm* of the gastro-vascular system with *ectoderm* of the surface in a ring all around the bell margin, and with it also the vascular lamella of the sensory niche, which has already been referred to in the general description of Charybdea. The lamellæ of the internal system have been described by previous writers, and especially by Claus in his paper on Charybdea, but they are still in need of comprehensive and clear treatment. The lamellæ of the margin and of the sensory niche have also been described by Claus, but not thoroughly or with entire accuracy, nor did he recognize the vascular lamellæ of the sensory niche as originally a part of the lamellæ of the margin. This last was first determined by H. V. Wilson upon specimens of Chiropsalmus quadrumanus obtained at Beaufort, North Carolina. Professor Wilson's unpublished notes on Chiropsalmus were very kindly placed in my

hands, and so far as the vascular lamellæ are concerned my own work is only a confirmation and amplification of his, since Charybdea and Tripedalia in this respect agree with Chiropsalmus.

The vascular lamellæ of the internal system are the most prominent and morphologically the most important. They comprise the four vertical strips of fusion that separate the four stomach pockets in the interradii (*ivl* in the figures of the series of cross-sections of Charybdea and Tripedalia, Nos. 6–15 and 21–29), and four curved horizontal cross-pieces at the top of these which separate the stomach from the stomach pockets, and would make the separation complete did they not leave in each perradius a free space between their ends, which makes possible the gastric ostia.

The arrangement of this internal system of vascular lamellæ is simple. What they amount to is a certain definite number of linear adhesions between the two walls of an originally undivided gastro-vascular space, by which that space is divided up into a central stomach and a peripheral portion, and the peripheral portion thus further divided into the four stomach pockets. Perhaps the idea may be conveyed by likening the whole medusa to a couple of bowls fitting closely one within another and plastered together at the margins. The exumbrella then would correspond to the outer bowl, the subumbrella to the smaller inner bowl, and the original undivided gastro-vascular space to the space between the two. If now the walls of the space be cemented together in four horizontal curved lines just in the plane where the bottoms are bending round to become the sides of the bowls, leaving four interspaces between the ends of the lines, we should have the original space divided into a central horizontal somewhat lens-shaped region between the bottoms of the two bowls that would correspond to the central stomach, and a peripheral vertical portion between the sides of the bowls that would correspond to the peripheral gastro-vascular system; central and peripheral portions would communicate by the four interspaces between the lines of fusion, which would correspond to the four gastric ostia. If, further, the vertical peripheral portion be subdivided by four more lines of fusion running vertically at equal distances apart, each connecting above with the middle point of the corresponding horizontal line of fusion, we should have the simple peripheral portion divided into four parts, corresponding to the stomach pockets, by four vertical lines of fusion, corresponding to the four interradial vascular lamellæ, the *ivl* of the figures.

These mutual relations of stomach, stomach pockets and lamellæ will perhaps be made clearer if a comparison is drawn between them and the similar structures of a Hydromedusa. Liriope, one of the Trachomedusæ, is a good form to take for such a comparison, since by reason of its direct development from the egg it is free from the complications of hydroid medusæ. The young medusa has at first a simple, undivided gastro-vascular cavity which later is divided up into the central stomach and the typical radial to circular canals of the Hydromedusæ by means of fusions between the two endodermal surfaces. Diagrams *a*, *b* and *c* of Fig. 35 represent very schematically this process of division into stomach and canals. In *a* we have a projection upon a plane surface of the primary, undivided gastro-vascular cavity, as seen from above; *b* shows the first four points of fusion in the interradii; *c* represents those four points expanded by growth in all directions into broad cathammal plates in such a way as to leave the stomach in the centre, the radial canals in the perradii, and the circular canal in the periphery as all that remains open of the primary simple cavity. These broad plates of vascular lamella, separating the narrow radial canals, persist in the adult Liriope to tell the tale of the formation of the definitive gastro-vascular system. It seems to me that we are justified by analogy in drawing a similar conclusion for the Cubomedusæ. In *d* of Fig. 35 is represented a projection of a Cubomedusa, in which the homology of the stomach pockets with the radial canals of the Hydromedusa, and of the narrow strips of fusion with the broad cathammal plates, is shown at a glance. To make the comparison more perfect we have only to remember that in the Cubomedusæ there exists below each interradial vascular lamella a connecting canal (Figs. 16, 29 and 35 *d*, *cc*) uniting the two separate adjacent pockets. This, as has been pointed out by other writers, is the representative of the circular canal of the Hydromedusæ. Practically the only difference between the structure of the gastro-vascular system of the Cubomedusæ and that of a form such as Liriope, is that in the latter the fused areas have broadened out at the expense of the radial canals, while in the Cubomedusæ on the contrary they have become long and narrow.

One is strongly tempted by the foregoing comparison to speculate a little as to whether the reproductive organs of the Cubomedusæ, which lie *in* the stomach pockets and are generally supposed to be endodermal, may not bear some closer relation to those of the Trachomedusæ, which lie "in the course of" the radial canals (Lang's Text-book) and by common

consent are ectodermal. And while we are being led by facts such as those just mentioned above to wonder just a little whether after all the position of the Cubomedusæ among the Acraspeda is so firmly assured—doubting some, yet in the frame of mind of one who "fears a doubt as wrong"—the velarium suggests itself as another point in question. Haeckel does not hesitate to state emphatically that the velarium of the Cubomedusæ and the velum of the Craspedote medusæ are only analogous, but the reasons that he gives (sie sind unabhängig von einander entstanden, und ihre Structur ist zwar ähnlich, aber keineswegs identisch; namentlich das Verhalten zum Nervenring ist wesentlich verschieden: System, p. 426) somehow do not produce so much impression upon one as the very velum-like appearance of the velarium itself. The origin from the fusion of marginal lobes is not as yet a matter of observation, and the relation to the nerve ring is not essentially different from that of the velum to the lower (*i. e.* inner) nerve ring in the Craspedotæ. The four frenula and the diverticula from the gastro-vascular system seem to be the chief differences in structure after all, and these Haeckel evidently did not think worth mentioning. This speculation, as to the possible relation of the Cubomedusæ to such forms of the veiled medusæ as Liriope, though it may be very tempting, is scarcely fruitful enough to repay much effort on the part of either reader or writer. The whole subject must remain uncertain until the facts of the development of the Cubomedusæ are known.

If the structure of the vascular lamellæ of the internal system has been made clear, the appearances of the vertical and horizontal components in the figures will be understood without much further explanation. The four vertical strips in the interradii (*ivl*) have been already referred to in the figures of the cross-sections of both Charybdea and Tripedalia. In the longitudinal sections of the two jelly-fish through the interradii, the vertical lamellæ are cut throughout their entire length from stomach to connecting canals (Figs. 5–20, *ivl*). The horizontal cross-pieces at the tops of the vertical lamellæ also appear in several of the figures. Fig. 36 represents the appearance that would be given by a longitudinal section taken through any portion of the upper part of the bell except in the interradii, or in the perradii, through the gastric ostia. The horizontal vascular lamella (*hvl*) is shown connecting the endoderm of the stomach (*ens*) with that of the stomach pocket (*enp*). In a longitudinal section directly through an interradius (Fig. 5 or 20) the horizontal lamella is cut just at the point where it joins the vertical, so that

the two are not differentiated. In a section through the region of a perradius (Fig. 4 or 19) the horizontal lamella is of course not cut, since the section passes through the gastric ostium, whose existence is conditional upon fusion not having taken place between the endodermal surfaces.

The first figure in each of the series of cross-sections (Figs. 6 and 21) also shows the horizontal vascular lamella, cut across slantingly twice in each quadrant as it passes between the gelatine of the ex- and of the subumbrella to connect the epithelium of the stomach with that of the stomach pocket. The fact that more of the lamella does not appear in such a cross-section only shows that its course is not perfectly horizontal.

The region in which the same lamella lies is indicated in the surface view of the top of the bell of Charybdea (Fig. 2) by the bent line *hvl* in each quadrant. The figure manifests the appropriateness of Claus's name for the horizontal lamella—"bogenförmige Verwachsungs-Streifen." Haeckel calls the same structures "Pylorus-Klappen," and in his account of Charybdea Murrayana in the Challenger Report, speaking of the three divisions of the stomach (buccal, central and basal) which he traces upwards from the stalked forms of Scyphomedusæ, he says: "The central stomach in this Charybdea, as in most Charybdea, is joined to the basal stomach, as the pyloric stricture between the two is not developed and only faintly indicated by the slightly projecting pyloric valves." Again, in speaking of the valves of the gastric ostia, he says: "These four perradial 'pouch valves' alternate with the interradial pyloric valves." It is difficult to understand, however, how the "bogenförmige Verwachsungs-Streifen" of Claus, which are undoubtedly the same structures as those which I have called the horizontal lamellæ, and are only strips of endodermal fusion, can be "projecting pyloric valves," or indeed can properly be spoken of as valves at all. Possibly Haeckel was not quite able to understand Claus's description, and in his desire to find something in the stomach of Charybdea which would serve to set off a central from a basal part, such as is found in the Lucernaridæ, hit upon Claus's "Verwachsungs-Streifen." I have elsewhere given it as my opinion that in such of the Cubomedusæ as I have studied there is no structure in evidence that would properly serve to mark a limit between a basal and a central portion of the stomach.

We have next to describe the marginal system. The vascular lamellæ mentioned above in every case connected endoderm of one cavity with endoderm of another; those of the margin have the noteworthy difference that they run from endoderms of some part of the

gastro-vascular system to *ectoderm of the surface.* The outermost cells of the endodermal lamellæ make direct connection with the ectodermal cells, without the usual intervention of a layer of gelatine.

The marginal lamella of Charybdea lies, as the name implies, just on the bell margin where the edge is curving round into the velarium. All around the whole circumference of the bell it is found (in Charybdea) at this same horizontal bend, except in the eight principal radii, where the tentacles and the sensory clubs have brought about modifications. In any place except these a vertical section through the margin will show the marginal lamella connecting the endoderm of the marginal pocket with the ectoderms of the surface, as represented by *vlm* in Fig. 38, which is a vertical section through the sensory niche a little to one side of the perradial axis.

In the interradii the marginal lamella undergoes modifications due to the fact that the bases of the pedalia are situated a little upwards from the exact margin, and that the lamella follows the outline of the bases. Fig. 1 shows one of the interradial corners of the bell margin looked at directly from the surface, so that the curved outline of the junction of the base of the pedalium with the exumbrella is seen. The trace made by the lamella where it meets the surface ectoderm follows this outline. The lamella is also shown in the vertical section through the interradius (Fig. 5 or 20, *vlm*), where it is seen running from the connecting canals (*cc*), which joins the two adjacent marginal pockets, upwards and outwards to meet the surface ectoderm. Its course from canal to surface is not in a direct line, but curved with the concavity upwards. Hence, in cross-sections at certain levels through the interradial corner it is met more than once and gives rise to appearances that seem at first sight too complicated for it to be just the same structure as the simple marginal lamella described above. That it is the same, and that the complication is only due to the insertion of the pedalia above the margin, can be determined by following through a series of cross-sections, the essential ones of which, as I hope, are given in Figs. 40–43. The levels of these are shown on Fig. 5 by the letters *w*, *x*, *y* and *z*, respectively. Fig. 40 shows the lamella cut but once, just below its highest part. The section is above the level of the connecting canal and hence still shows the vertical interradial lamella *ivl*. Fig. 41, at the next lower level (*x*), shows the same portion of the lamella intersected a little nearer the interior, while the junction with the endoderm of the connecting canal is shown still further inside. Fig. 42 is at level *y*, just through the

bend of the loop, so that in part of its course the lamella is cut almost horizontally, *i. e.* in its own plane. Fig. 43 finally shows the lamella as it appears below the level of the connecting canal, cut twice, each portion joining endoderm of marginal pocket with ectoderm of surface. It thus bears exactly the same relations that it had when we first met it in Fig. 38 (*vlm*), except that here in Fig. 43 one finds that a cross-section cuts it at right angles instead of a vertical as in Fig. 38, as a result of its being pushed upwards from its former position on the margin by the insertion of the pedalium above the margin.

The vascular lamella of the sensory niche has already been alluded to as part of the marginal system, and brief reference has been made to it in the section on the sensory clubs. Like the rest of the marginal lamella, it connects endoderm with ectoderm. The line that its fusion with the ectoderm traces on the surface frames in a shield-shaped area at the bottom of the sensory niche, which is seen in the drawing of the outlines of the niche, Fig. 44 (*vls*). This lamella was observed by Claus, and was figured by him both in surface view and in cross-section through the niche. Apparently, however, he omitted vertical sections through the niche, so that he supposed that the outline traced by the lamella was not continuous above, *i. e.* over the stalk of the sensory club ('78, Fig. 41; text, p. 28). That the outline is closed above, though masked in surface view by the roof of the sensory niche, is seen at once in vertical sections, such as Figs. 37 and 38, one of which is directly through the perradius, the other a little to one side. Both show the vascular lamella of the sensory niche (*vls*) intersected twice, above and below the sensory club, and completely cutting off the exumbrella from any share in the bottom (or inner wall) of the sensory niche. Fig. 39, which is a cross-section through the upper part of the niche, and is essentially like the similar figure of Claus, shows in like manner that the bottom of the sensory niche belongs to the subumbrella. H. V. Wilson was the first to point out, in his unpublished notes, that the lamella of the niche is complete all round.

In the adult structure of Charybdea and Tripedalia the lamella of the niche is connected with that of the margin by a vertical strip of endodermal fusion that does not come to the surface like the rest of the marginal system, but remains just internal to the gelatine of the exumbrella, connecting the two adjacent marginal pockets. In the cross-sections of Charybdea it is seen in Fig. 16 (*vlc*); in those of Tripedalia it is seen in Figs. 28 and 29. In vertical section it is found in Figs. 4, 19

and 37. In Fig. 44, which represents the bell margin and velarium of Tripedalia arranged as if the velarium were vertical and pendant from the margin (instead of suspended by the frenulum so as to be at right angles to the vertical plane), the connecting lamella is shown as a dotted line (*vlc*)—dotted because it does not come to the surface—joining the lamella of the niche with that of the margin (*vlm*).

The same figure (No. 44) shows a characteristic difference between the marginal lamella of Tripedalia and that of Charybdea. While in Charybdea, as Claus points out, the marginal lamella keeps at one level, just a little above the bell margin, all the way round (except where disturbed by the special modifications of the tentacles and the sensory clubs), and never descends into the velarium, in Tripedalia on the other hand it describes a sinuous course, following the outlines of the marginal pockets, as is indicated in the figure by the light parallel line *vlm*. The course as it would be seen in a surface view is obscured just at each side of the interradius by the overhanging of the bases of the two lateral pedalia. This is why the lamella is not indicated at these points in the diagram. The course is seen to lie almost wholly on the velarium, that is, in the figure below the line which represents the bell margin proper, the line at which the angle comes when the velarium is in its normal position, horizontal to the vertical side of the bell.

In this sinuous course of the marginal lamella we have another point of resemblance between Tripedalia and the Chirodropidæ. H. V. Wilson worked it out in his sections of Chiropsalmus, and the reconstruction which I have given in the figure under discussion is in all essentials similar to his for Chiropsalmus. The differences lie only in the fact that Chiropsalmus has more velar canals, and that the chief marginal pocket in each quadrant is not forked peripherally, as is that of Tripedalia (*mp*), but presents its distal margin parallel to the edge of the velarium. The two smaller marginal pockets in the perradii (*mp'*) are on identically the same plan in both.

Tripedalia, having three tentacles joining the umbrella in each interradius, shows a disturbance of the course of the marginal lamella in these regions by just so much the more complicated than in Charybdea. The plan, however, is exactly the same. The lamella is pushed upwards from the margin by each of the bases of the three pedalia just as is done by the base of the single pedalium of Charybdea. Fig. 29 shows the lamella in the same relation to the canal of the central tentacle (*ct*) that it has in the similar sections of Charybdea (Figs. 16 and 43); and in

addition the first appearances (as the series is traced downwards) of the arches of the lamella over the two lateral tentacles (*cl'*), which are inserted a little lower down than the middle one of the group. As concerns these lateral tentacles, the relations of the vascular lamella at this level are the same as that in the level of Fig. 40 for Charybdea.

It has been stated more than once already that the vascular lamella of the sensory niche is a part of the lamella that runs round the margin, and so far the only evidence given has been the strip of endodermal fusion running from the marginal lamella to that of the niche. This strip, however, as has been described, does not come to the surface and consequently seems at first sight to be a different structure from the lamella of the margin. That it is not, however, I found very prettily shown in a series of sections of one of my youngest Tripedalia. In this the lamella of the niche as it was traced in successive sections downwards, was found not to form a closed ring at the bottom of the niche, but each side was continued directly and separately downwards to the margin, where it passed into the corresponding part of the marginal lamella. A reconstruction of the condition, similar to that of Fig. 44, is given in Fig. 45, and I think explains itself at a glance. Evidently the vascular lamellæ that connect the lamella of the sensory niche with that of the margin at first come to the surface, like the rest of the marginal system, but as the animal grows older come to lie within the gelatine. In this way the condition found in cross-sections just through the margin of my very small Tripedalia, and represented in Fig. 46, becomes that of the adult seen in the corresponding portion of Fig. 29. It is as complete a demonstration as could be required that the lamella of the sensory niche is at first only a loop of the marginal lamella, a conclusion that had been already reached by H. V. Wilson on theoretical considerations, based upon the facts of the adult structure as he found them in Chiropsalmus.

As Wilson pointed out in his notes, these facts have a close bearing upon the question of the origin of the velarium. Sixteen marginal pockets are found in both Chiropsalmus and Tripedalia, and all of them extend into the velarium. It is not unnatural to suppose that these belong to sixteen marginal lobes, and that these lobes have fused together to form the velarium. In the Chirodropus figured by Haeckel (Taf. XXVI) in his "System" gelatinous lobe-like thickenings are shown in the velarium, corresponding to the sixteen marginal pockets. In Tripedalia no special gelatinous thickenings are found, but the arrangement of the marginal pockets is the same as that of the Chirodropidæ, and

perhaps I ought, when treating of the systematic relations of Tripedalia (p. 5, Fam. III), to have recognized the analogy to the extent of saying that marginal lobes may not be completely absent from the velarium of Tripedalia. At any rate the gelatinous lobes in the case of Chirodropus on the one hand, and on the other hand the sinuous outline of the margin still mapped out by the lamella in Chirodropus, Chiropsalmus and Tripedalia, are certainly very suggestive of an ancestral Cubomedusa in which there was no velarium, but sixteen free marginal lobes instead. Two more indications favor slightly the same view. In both Charybdea and Tripedalia a small notch is seen in the edge of the velarium in the perradius (Fig. 44). Its constancy suggests that it may not be a chance or meaningless feature. The second point is the small size of the two marginal pockets adjoining the perradius. These are in the position of the ephyra lobes of the Discomedusæ, which always lie on either side of each sensory club, and which do not keep pace with the other marginal lobes in development. In the Rhizostome jelly-fish especially they are found much smaller than the other lobes, as will be seen by a glance at such figures as Haeckel's for Lychnorhiza (System, Taf. XXXIV, Fig. 2), or for Archirhiza (Taf. XXXVI, Fig. 5), or Hesse's figure of the margin of Rhizostoma Cuvieri ('95, Taf. XXII, Fig. 22). The resemblance between such margins and that of Tripedalia (Fig. 44), with its simple, unbranched velar canals, is very suggestive. On the other hand it must be remembered that in considering the vascular lamellæ of the internal system we found the indication pointing rather more to Hydromedusan affinities than to any other. Charybdea throws no light on the question, since it has no marginal lobes on the velarium and the marginal pockets end strictly at the margin, so that the only diverticula of the gastro-vascular system in the velarium are the velar canals.

Before leaving the subject of marginal lobes and pockets I must answer a possible objection that may occur to some careful reader. It may seem that I am wrong in holding that there are two marginal pockets in each octant instead of three, that just as there is one velar canal from each of the smaller perradial pockets (*mp'*, Fig. 44), so each prong of the forked larger pocket (*mp*), since it is continued into a velar canal, ought to be called a marginal pocket likewise, the whole number of marginal pockets then being twenty-four instead of sixteen. Such a revision of the terminology would not be without some reason in its favor, and perhaps a study of more forms would show it to be correct. But for the present, at any rate, it seemed to me best to abide by the analogy of

Chiropsalmus, in which the peripheral edge of the larger marginal pocket in each octant is not bow-shaped, but runs parallel to the edge of the velarium. A revision of the terminology of the marginal pockets such as implied in the suggestion above would also give rise to complications when applied to Charybdea, since the latter has no marginal pockets in the velarium.

As to the functions of the vascular lamellæ, there is too little known to say much. It is rather improbable that structures retained so definitely should be mere scaffolding left over from a previous stage of usefulness. Claus has found in Chrysaora that the lamellæ form a kind of capillary network in communication with the gastro-vascular system, and he with others supports the view that they perform an accessory function in the nutrition of the tissues they penetrate. Upon this point I have no observations of my own to add.

The marginal vascular lamella is regarded by Claus as perhaps the vestige of a circular canal around the bell margin. On this subject, too, I have nothing to add. A lamella of endoderm that connects directly with the ectoderm of the surface along its whole course is a structure whose meaning I am wholly unable to understand or even to guess at. A similar lamella is described by Hesse ('95, p. 430) as occurring in the ephyra lobes of his Rhizostoma, and he mentions Eimer as the first to discover this structure, probably meaning the first to discover it in the Discomedusæ. Whether the lamella is found all around the margin is not stated. Hesse refers it to the ephyra, and remarks that the investigation of it in the ephyra would undoubtedly give interesting results.

I will close this part upon the vascular lamellæ with a very pertinent suggestion made by Professor Brooks to the effect that the usual way of speaking of the sensory clubs as having moved up from the margin is looking at the matter in the wrong way. The level of the sensory clubs undoubtedly represents the original margin, which elsewhere has grown down and away from its former level, leaving the sensory clubs like floatage stranded at high-tide mark. Only in this way can the lamella of the sensory niche have any meaning.

B: The Nervous System.

The nervous system of the Cubomedusæ is the most highly developed that is found in any of the jelly-fishes. If the position of the group among the Acraspeda is established, it alone is ample to prove that the Hertwigs had not sufficient evidence when they stated in their mono-

graph on the nervous system of the Medusæ ('78) that the Acraspeda show a much lower nervous organization than the Craspedota.

The system naturally groups itself under three heads, the nerve ring, the sensory clubs, and the motor plexus of fibres and ganglia that underlies the epithelium of the subumbrella. The general relations of the nerve ring and of the sensory clubs have been given before in the description of Charybdea Xaymacana, so that we may pass at once to the consideration of the finer details of the nervous tissues.

In the structure of the nerve ring I have found myself unable to come to the same results as those given by Claus, who so far as I know is the only one that has studied the nerve with special reference to its histology. Our difference amounts to this, that he finds two distinct types of cells in the epithelium of the nerve, sensory and supporting, which would make it a receiving as well as transmitting organ, while I have not been able to demonstrate satisfactorily the sensory cells, and, therefore, so far as my own observation is concerned, I am disposed to attribute to the nerve simply the function of conducting impulses. I do not know just how much weight to assign to my inability to find evidence in my sections of the sensory type of cells. Eimer (mentioned by Hesse, '95, p. 420), the Hertwigs ('78) and Claus ('78) have independently discovered the two types in one medusa or another, and the Hertwigs, at least, have demonstrated them by macerated preparations. So far as Charybdea is concerned, however, Claus had only preserved material and had to rely upon sections, as have I, since the material which I had preserved with especial reference to maceration did not turn out well. The results that we get from sections vary enough for me to believe that Claus interpreted his sections very much by analogy with other forms—as indeed, is suggested by his own words ('78, p. 22): "Da es mir nicht geglückt ist die durch die längere Conservirung in Weingeist fest vereinigten Elemente zu isoliren, habe ich das muthmassliche Verhältniss beider Elemente nach Analogie der mir für die Acalephen bekannt gewordenen Verhältnisse, welche O. und R. Hertwig so schön auch am Nervenring der Carmarina zur Darstellung gebracht haben, zu ergänzen versucht." There can be no doubt of our having the same structures to deal with, for C. Xaymacana is so much like C. marsupialis as to be perhaps more worthy of being called a variety of the latter than a distinct species.

The structure of the nerve as I conceive it is given in Figs. 47 and 48. The former represents a cross-section, and shows, as others have pointed out, that the layer of circular muscle fibres (*cm*) is interrupted by

the nerve. It is evident that the tissues which elsewhere on the subumbrella were differentiated into muscle epithelium and muscle fibre have here become nerve epithelium and nerve fibre, a point that has not been remarked upon before, so far as I remember, and that may be of interest in connection with the neuro-muscular theory. The epithelium of the nerve (*scn*) is seen to be made up of cells whose inner ends narrow down into a kind of stalk or process that runs to the gelatine of the supporting lamella (*gs*) and there joins a little cone of the gelatine that juts out to meet it. The cells are smaller in general than those that overlie the muscle layer, especially on the two lateral margins of the nerve, where they are more crowded together and overarch the nerve-fibres. The fibres are seen in cross-section between the processes of the cells. They apparently must lie imbedded in some clear, watery fluid that does not show in the preserved material. The processes of the epithelial cells give the fibres the appearance of lying in alveoli, or being divided into strands, and one of these strands (*ax*) is always discernible among the others by reason of its more numerous or finer or more compactly massed fibres. This is the "axis" of Claus. Here and there in its course appear ganglion cells having their long axis in the longitudinal direction of the nerve. Elsewhere, in the nerve as well, and usually nearer to the surface, are found other ganglion cells, mostly bipolar, some multipolar, which are readily distinguishable from those of the axis by the fact that their long axis lies across the nerve. One of these cells is shown in the figure (*gc*). Here and there in the epithelium alongside the nerve are found mucous cells (*mc*), distinguished by their clear contents and by the small exhausted-appearing nucleus at the base with a few threads of protoplasm.

In Fig. 48 I have tried to represent the structure of the nerve by means of a series of five different views such as would be given by focusing at five successive levels. In the first (1) we have the epithelium of the nerve (*scn* in Fig. 47) in surface view, the cells appearing polygonal in outline, with here and there a mucous cell. In (2) we find a very slight layer of ganglion cells and fibres having a transverse direction (*gc* and *fp* in Fig. 47). These are continuous with the plexus of fibres and ganglion cells which lie above the muscle layer all over the subumbrella, and which represent the motor part of the nervous system. This connection with the nerve shows how co-ordination is effected. At the same level are found fibres of the axis also having a longitudinal direction. In (3) is seen the main body of fibres, divided in the osmic preparation

from which the drawing was made into irregular wavy strands which are in all probability largely the result of preservation, but are in part also due to the separation by processes of the epithelial cells, as was seen in Fig. 47. The axis is seen with one of its longitudinally directed bipolar ganglion cells; and at the sides the fibres of the circular muscle of the subumbrella. These show a slanting direction to the nerve, due to the fact that the nerve, as mentioned before, has a sinuous course from the margin in interradius to the level of sensory club in perradius. At the next focus (4) we come to the gelatine of the subumbrella (*gs* in Fig. 47), and below this (5) to the larger polygonal outlines of the endodermal cells of the stomach pocket (*enp*, Fig. 47), which like the ectoderm show mucous cells at irregular intervals.

A comparison, now, with Claus's figures ('78, Taf. II, Figs. 19–21) will show that, except for the rather unimportant matter of the mucous cells, which he finds regularly and thickly disposed on each side of the nerve ('78, Fig. 21), our only essential difference lies in the matter of sensory cells in the epithelium. His figures show a multitude of spindle-shaped sensory cells whose central ends are continued in processes that bend around into the mass of fibres of the nerve. In his Fig. 20 a relatively small number of nuclei, just one-third as many, are seen attached nearer to the surface, which represent the supporting cells. The plan of structure (as shown in his Fig. 20) is an alternation of (1) supporting cells offering a broad peripheral end to the surface and having the central end continued as a supporting fibre to the gelatinous lamella, and (2) spindle-shaped sensory cells with nuclei at a lower level, which send their peripheral process up between the supporting cells to the surface, while the central process becomes continuous with the nerve fibres, often branching into two processes. In my sections I have not been able to see either a regular alternation of nuclei at different levels, or central processes which unmistakably bend round into the nerve fibres. In every case in which I could trace the central process of a cell clearly it ran to the supporting lamella, and this whether the nucleus of the cell lay near the surface of the nerve or deeper down, as in the somewhat spindle-shaped cell seen on the left of the centre of the nerve in Fig. 47. Of course in many cases the central process could not be traced in a section, and this leaves room for the supposition that such were always the sensory cells. From my inability to demonstrate sensory cells in the nerves of Charybdea, I by no means wish to deny their existence; for that remains to be proved, or disproved, by macerations. At any rate,

they cannot be so numerous as has been supposed. The position of the nuclei shows that.

The epithelium of the nerve is said by Claus to be ciliated. It has been suggested by Schewiakoff that probably in such cases the sensory cells bear one long cilium, while the supporting cells have many smaller cilia. Unfortunately, I made no observations upon the ciliation of the nervous structures of the living animal, and the traces of cilia that are shown in preparations of preserved material are a poor basis to speculate much on. Claus considers the sensory cells of the epithelium of the nerve a special seat of tactile sensation.

The way in which the nerve reaches the sensory clubs is interesting. Under the topic of the vascular lamellæ it was explained that the sensory clubs and the bottom of the sensory niche from which they spring are parts of the subumbrella. Fig. 37 reminds at a glance better than any other one drawing how the bottom or inner wall of the niche is completely cut off from the exumbrella by vascular lamellæ above and below the stalk of the club. From this figure, now, it will readily be understood that the nerve in order to pass to the base of the stalk has simply to traverse the gelatine of the subumbrella. This fact, which seems surprising enough at first sight in view of the position of the clubs on the external surface of the umbrella, was correctly pointed out and explained by Claus, but one or two figures will serve perhaps to give a clearer idea of it.

Fig. 49 is a diagram of the nervous structures in the region of the sensory niche, as they would be seen on the surface of the subumbrella turned toward the bell cavity. The outline of the sensory niche as it is seen through the tissue of the animal is represented by the line *osn*. The sensory club (*scl*), and its stalk with a conical basal portion are given by the lightly dotted outline and are also imagined as seen through the animal. The nerve (*n*), being on the surface of the subumbrella, is shown as a heavy line describing an arch over the outline of the niche. In the middle point of the arch is a slight thickening of the nervous tissue (*rg*) which shows in section a large increase in the number of ganglion cells, and is the radial ganglion of Claus. The same is seen, exaggerated in size, in Fig. 12. From it there extends upward a slender strand of nervous tissue (*rn*), the radial nerve of Claus. In Charybdea this can be traced but a very short distance. In Tripedalia it is much more distinct and traceable for a longer distance, and I might say in passing that this and the sensory organs in the proboscis are the only differ-

ences I have noted between the nervous systems of Tripedalia and Charybdea.

Nerve ring, radial ganglion and radial nerve all lie on the bell cavity surface of the subumbrella. The way, now, in which the nerve ring reaches the base of the stalk is simply by sending two roots through the gelatine of the subumbrella to the conical base of the stalk. These roots are seen in the diagram at *rns*. After passing through the gelatine the roots come together on the inner side of the base—that is, the side turned toward the bell cavity—and then pass downwards (*nst*) on the inner side of the stalk of the club to the mass of nervous tissue at its end.

This passage of nervous tissue through the gelatine in order to reach the sensory club is a little hard to grasp at the first, and I have tried to render it more intelligible by a couple of drawings of sections. Fig. 50 is a transverse section through the upper part of the region of the sensory niche, not quite horizontal (*i. e.* parallel with the bell margin), but slanting so as to lie on the plane of the reference arrow *x–y* in Fig. 49. The plane passes just through the top of the niche, and in two areas has cut through the roof with its epithelium of ectoderm (*ece*, *ecs*) so that the space of the sensory niche (*sn*) appears. The vascular lamella of the sensory niche (*vls*) is shown, as in Figs. 13 and 14, running on each side from the endoderm that lines the canal of the sensory club (*enc*) to the endoderm of the adjacent stomach pocket (*enp*). By it the gelatine of the exumbrella is separated from that of the subumbrella, and one sees that it is only through the latter that the nerve has to pass in order to reach the base of the sensory club. It is also seen that one part of the roof of the niche which is cut through lies outside of the ring of lamella and is therefore lined with ectoderm of the exumbrella (*ece*) while the other lies within the ring and is lined with ectoderm of the subumbrella (*ecs*). Owing to the slanting direction of the cut only the root on one side is cut through. The other is indicated, however, on the right side of the drawing. In this method of passage of nerve fibres, together with the accompanying ganglion cells, directly through the gelatine to the stalk of the sensory club my work is only confirmation and explanation of Claus.

Fig. 51 is a vertical section through the base of the stalk in the plane of the reference arrow *w–z* in Fig. 49, and therefore passing through one of the roots of the nerve of the stalk. Here again the region is seen to be cut off from the exumbrella by the vascular lamella of the sensory niche (*vls*), and the nerve is seen passing through the gelatine

of the subumbrella from the surface of the bell cavity (*sc*) to the base of the stalk hanging in the sensory niche (*sn*). One of the ganglion cells (*gc*) that accompany the nerve is seen to have two nuclei, a not infrequent occurrence which has been pointed out by others.

The same figure shows that the axis (*ax*) of the nerve has penetrated the gelatine with the other fibres. Here at the base of the stalk it takes a horizontal course and becomes directly continuous with the similar structure of the other root, as Wilson, I believe, first pointed out. This part of the nervous tract which runs horizontally along the base of the stalk between the two roots (Fig. 49, *rns*) has been considered by Claus the representative in Charybdea of the upper nerve ring of the Craspedota, which therefore exists in Charybdea in four separate portions. Seeing, however, that the region in which it is found belongs to the subumbrella, the homology seems very doubtful. Moreover, the fact that the axis of the nerve ring runs through this outer portion, instead of remaining on the inner surface of the subumbrella and passing to the radial ganglion, rather indicates that the outer portion is part of the original course of the nerve ring, while the portion that remains on the inner surface is perhaps a later formation.

A very interesting feature of the nervous system occurs in the same region in the form of a tract of fibres underlying the endoderm, and separated from the other fibres by the gelatine of the supporting lamella. It is seen in vertical section in Fig. 52 (*enf*), which is a section through the base of the stalk in just about its median plane, and, therefore, to one side of the arrow *w–z* in Fig. 49 and the corresponding drawing, Fig. 51. In cross-section it is represented also in Fig. 50 (*enf*). It varies in size and prominence very much in different specimens. Fig. 52 is a camera drawing of it in the case that showed it most developed. Ganglion cells are found in it, but comparatively infrequently. In some cases the tract itself can hardly be found with certainty. Hesse has described in a Rhizostome a much more highly developed tract in a corresponding position on the base of the marginal body. Fibres from the "outer sensory pit" pass through the gelatine to the sub-endodermal tract, which is described as surrounding the epithelium of the canal of the marginal body like a collar and is most thickly developed on the under surface of the canal, at the place that just corresponds with the point where, and where only, I find the tract in Charybdea. Hesse thinks that fibres then pass from this region to the nervous epithelium of the "inner sensory pit" lying underneath the base of the marginal body, which

contains a rich supply of ganglion cells and is considered by him to be the centre of the nervous system of the medusa. A close comparison cannot be drawn with Charybdea in this matter, however, since Charybdea has nothing to correspond with the "outer" and "inner" sensory pits. Moreover, the endodermal tract is not found encircling the canal of the sensory club, nor could I trace fibres passing from it through the supporting lamella into the fibres of the nerves.

Claus has figured ('78, Taf. V, Fig. 45, *Fb*) a small bundle of fibres in the stock of the sensory club lying between the endoderm cells of the canal and the supporting lamella. The same bundle is found in both Charybdea and Tripedalia and can be traced in cross-sections up the stalk to a point which must correspond with that at which the endodermal tract is seen in Fig. 52. Downwards it can be traced only as far as the entrance of the stalk into the knob of the club where it invariably becomes lost to view. According to Hesse ('95, p. 427) Schäfer found under the endoderm cells of the whole stalk of the marginal body a fibrous layer like that under the endoderm cells which he refers to slender processes from the cells of the crystalline sac. Although Hesse, as we have seen, finds the layer more limited in extent than Schäfer gives it, and does not trace it to the same source, the observation of Schäfer seems to me worthy of mention here, inasmuch as the trend of the fibrous bundle under the endoderm cells of the stalk in Charybdea and Tripedalia suggests quite strongly that the fibres come from the crystalline sac, as Schäfer thought to be the case in his medusa.

Besides the radial ganglion situated in the course of the nerve ring at its four perradial points there are four other similar ganglia on the subumbrella. These lie in the interradii, at the four lowermost points of the nerve's course, and undoubtedly send off nerves into the pedalia at whose bases they are situated. F. Müller ('59), whose work was not accessible to me, is quoted by Claus as recording two ganglia opposite the base of each pedalium which gave off a great number of nerves partly into the velarium, partly into the tentacles. Claus observed nothing of the kind in Charybdea and states that even the interradial ganglia do not exist.

That they do, however, is shown without doubt in sections of both C. Xaymacana and Tripedalia, but nerves to the velarium or to the tentacles I was unable to find.

On the two sides of each frenulum and of each suspensorium are found sub-epithelial ganglion cells in greater numbers than elsewhere on

the subumbrella, and I am inclined to ascribe to them also the importance of special ganglia controlling the musculature of the frenula and suspensoria. Certainly such ganglia would not be out of place.

It has been mentioned that the greater prominence of the radial nerve and the possession of special sensory organs in the proboscis were the only points of difference I had noted between the nervous systems of Charybdea and Tripedalia. These sensory organs remain to be described. They are simple ciliated cysts containing a concretionary mass, and are situated in the gelatine of the proboscis, irregularly disposed of at any level, from the lips to the beginning of the stomach, and in any radius. In one series of the adult animal fifteen were counted, of which seven were situated about interradially, four perradially, two adradially and two subradially. In another, twenty-one were counted, twelve in the perradii and nine situated between the sub- and perradii. The one shown in Fig. 24 is in the perradial position, often seen. In the sections of the very young Tripedalia in which the vascular lamella had not reached the adult condition the sensory organs of the proboscis were not found, although the sensory clubs showed practically no difference from the adult. Their structure is very simple—merely a round or oval sac lined with ciliated cells which bear up and keep in constant motion an irregular coarsely granular concretion. Fig. 53 is a sketch made in Jamaica from the living specimen. Sections were somewhat disappointing in that they added but little. Fig. 55 was drawn to show that now and then a mucous cell (*mc*) is found among the other cells of the sensory epithelium. An irregular-shaped mass (*rc*) was always found inside the cysts as the organic remains of the concretion. It gave no trace of cellular structure and offered no evidence whether the concretion was the product of one or few or of all the cells of the cyst. The latter would be unique among the medusæ. Even if the otocyst is the result of the activity of only one or a few cells, it is, so far as I know, the only case known for the jelly-fish of a free, unsuspended concretion.

As to whether the cysts are of ectodermal or endodermal origin could not be determined, but there was some evidence in favor of the latter. Fig. 56 is a drawing of one seen in optical section in a whole mount of part of a proboscis, and shows a definite connection with the endoderm of the proboscis. This was the only case when such connection was satisfactorily established, but in sections it was not uncommon to find what seemed to be the remains of the broken stalk, as in Fig. 54 (*rs?*). No connection could be traced between the cysts and any other

part of the nervous system. As to function, the idea that they serve to give perception of space relations suggests itself as readily as any other hypothesis.

We come now to the consideration of the terminal knob of the clubs, the sensory portion proper. A complete and detailed account of the complex structure of these organs would fill many pages and involve much useless repetition. Claus ('78) has described them with accuracy, but not in great detail, and since then Schewiakoff ('89) has given a careful general description and has supplemented Claus's work by observations upon the finer structure made with the aid of more recent technique. It seems in place for me, therefore, to give in the briefest possible way a general idea of their structure, and to pass then at once to the points in which my work has led me to different conclusions from those of Claus and Schewiakoff. In brief, then, the knob of the sensory club consists of a thick, complex mass of nerve fibres, more or less imbedded in which lie the special sensory organs, surrounding the ampulla-like terminal enlargement of the canal. The surface between the special organs is covered with less specialized sensory epithelium. The sensory organs are seven in number. Of these, four are simple invaginations of the surface epithelium arranged in two pairs symmetrically to the median line in the proximal end of the knob (the end where the stalk enters) and having pigment developed in the cells so invaginated, while the space of the invagination is filled with a gelatinous refracting secretion. These are considered simple eyes. Two more of the organs are complex eyes situated on the median line of the inner surface of the knob, the upper one smaller than the lower, but having almost exactly the same structure. Each has a cellular lens over which extends a superficial, corneal layer of cells; below the lens a refractive "vitreous body"; and below this a retina with pigmented cells. The seventh organ is the crystalline sac, which lies almost at the end of the knob opposite to the stalk and contains a large concretion. In view of the fact that the sensory clubs *in toto* have been abundantly figured by Claus and Schewiakoff, it is my intention to give but one simple figure of the general relations, and I justify that one in that it was made from the fresh material. Fig. 57 is a camera sketch of the outlines given by a sensory club seen in optical section from the side. The smaller upper and the larger lower complex eyes which are situated on the mid-line, are seen in profile, while the two small simple eyes give the outlines that they would in a surface view of their side of the knob. Of course it is understood

that two similar ones would appear on the other side, since the four simple eyes are symmetrically paired on either side of the mid-line. The sketch seems to show at least this much, that even in the living state the lens of the larger eye projects out beyond the other contours of the surface, so that the marked convexity ascribed to it in descriptions is not to be attributed to the preservation.

It is in reference to the structure of the retina and vitreous body of the complex eyes that I have found myself unable to come to the same conclusions as Claus and Schewiakoff. Since the work of the latter goes much further into the detail of the subject than does Claus's paper, it will be sufficient for me to compare my results simply with those of Schewiakoff.

The latter finds that the retina is composed of two kinds of cells, corresponding to the supporting and sensory cells referred to in the description of the nerve ring. These he figures ('89, Taf. II, Figs. 12 and 13) as alternating regularly. The two kinds of cells differ as follows:

(1) Shape. The supporting cells like those referred to before, are cone-shaped, having a proximal fibrous process that runs into the underlying stratum of nerve fibres, and on the surface of the retina a broad distal pigmented termination. The sensory cells are spindle-shaped, the proximal processes becoming continuous with fibres of the underlying nervous mass, while the distal process runs up to the surface of the retina (the part toward the lens) in between the ends of the supporting cell. The two kinds of cells are accordingly designated as pigment and visual.

(2) Position of nucleus. This comes in as a corollary of the shape. The nuclei of the visual cells lie in the enlarged central part of the spindle-shape, and, therefore, at a lower level than the nuclei of the alternating pigment cells.

(3) Processes in the vitreous body. The distal processes of the spindle-shaped visual cells are continued through the vitreous body to the cells of the lens as rod-like visual fibres which lie in canals in the (supposedly) homogeneous vitreous body. The pigment cells on the other hand have no fibres passing from them through the vitreous body, but in the latter are situated cone-shaped masses of pigment whose bases rest upon the broad ends of the pigment cells without, however, being a part of the cell.

(4) Pigment. The distal ends of the pigment cells in the retina are strongly pigmented, as the name implies. The processes of the visual

cells, which alternate with these, are pigmented likewise, but the pigment is not so abundant and lies in the periphery of the cell body, leaving free a highly refracting central axis.

If the relation of these cells to each other has been made sufficiently clear, it will be understood that, in accordance with Schewiakoff's scheme of the structure, sections that cut the retinal cells transversely give very different appearances at different levels. A section through the very tops of the retinal cells, that is, the last section of the retina before striking the vitreous body, would show large polygonal areas of heavy pigment (the ends of the pigment cells), in between which would lie the much smaller, less pigmented, highly refracting ends of the visual cells ('89, Taf. II, Fig. 19). A section lower down in the retina, that is, more toward the centre of the club, would strike the low-lying enlarged central portion of the visual cells with their contained nuclei, and the smaller, proximal ends of the pigment cells. It would, therefore, give the reverse appearance from the preceding section, namely, that of large unpigmented (or but slightly pigmented) areas (the swollen bodies and nuclei of the spindle-shaped cells), and in between them smaller pigmented areas, the ends of the proximally tapering pigment cells ('89, Taf. II, Fig. 20). A section on the other side of the one first described, that is, one of the first through the vitreous body, would show pigment areas of the same size as the large ends of the pigment cells (the cone-shaped streaks of pigment in the vitreous body which according to Schewiakoff are associated with the pigment cell), and in between them the cross-sections of the rod-like processes from the visual cells, lying in canals in the clear homogeneous ground-substance of the vitreous body ('89, Taf. II, Fig. 18).

Let me give a resumé of Schewiakoff's conception of the structure of the retina.

a. There is an alternation of pigment and visual cells, the nuclei of the spindle-shaped visual cells lying at a lower level than those of the cone-shaped pigment cells.

b. From the visual cells extend rod-like processes into the vitreous body, lying in canals in the latter.

c. In the vitreous body a cone-shaped streak of pigment overlies each pigment cell of the retina, which is not a part of that cell.

d. Apart from these pigment streaks and the rod-like processes of the visual cells the vitreous body is structureless, probably a secretion of the pigment cells.

My own work, now, has led me to a different conception, so that my conclusions on the same points would be as follows:

a. There is not good evidence of an alternation of cone-shaped pigment cells and spindle-shaped visual cells, with the nuclei of the latter at a lower level than those of the former.

b. From some of the retinal cells otherwise not distinguished, there extend rod-like processes into the vitreous body, such as described by Schewiakoff.

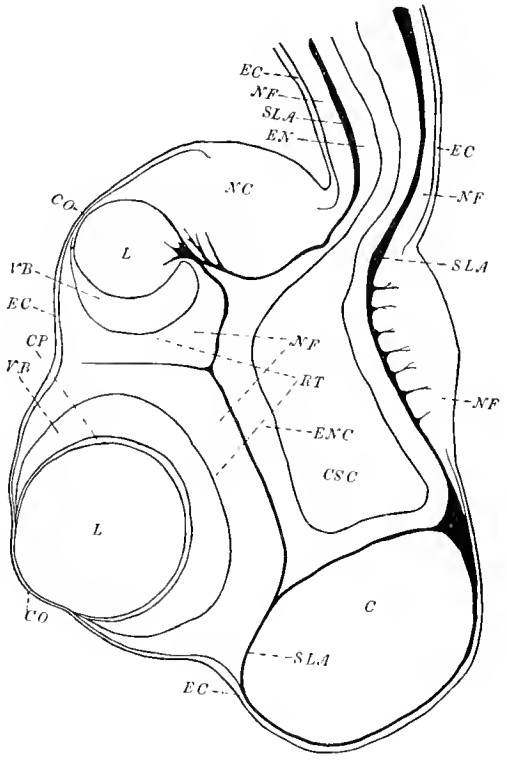
c. The cone-shaped streaks of pigment in the vitreous body belong to the underlying pigment cells, in fact are direct continuations of them, and at their distal ends they are prolonged into fibrous processes lying in canals of the vitreous body exactly like the visual fibres of Schewiakoff.

d. The vitreous body is not a homogeneous secretion, but is composed of prisms of refracting substance, each with a denser central fibre.

Let us go over these four points in detail.

(a) As to the first, the question whether there is an alternation of pigment and visual cells, I am not prepared as yet to make a positive statement, since my not seeing both kinds as they are described has little evidential value against the fact that Claus and Schewiakoff both claim to have seen them. Perhaps proof could be obtained one way or the other by maceration of fresh or of specially prepared material, which none of us had. My evidence for not confirming alternation rests wholly upon sections. Fig. 58 represents a radial section through part of the larger eye of Charybdea, made from an osmic preparation which in this case showed two advantages over the material fixed in corrosive-acetic (usually by all odds the best), namely, that the vitreous body (*vb*) was not shrunken away from the retinal cells, as almost invariably happens, and that the retinal cells were contracted apart from one another in some places in such a way as to be almost equal to a macerated preparation. Now, in the figure it is seen that there is an apparent alternation of two kinds of cells, more regular than I usually find, but the ones that are undoubtedly the pigment cells of Schewiakoff are the ones that show the fibrous processes like his visual cells, and the pigment streaks in the vitreous body are seen to be integral parts of the cells, not cone-shaped masses lying in the vitreous body, merely associated with the pigment cells. If these *are* the pigment cells of Schewiakoff, the shorter cells in between must be his visual cells, yet they can by no means be said to conform to a spindle-shaped type, nor are their nuclei always at a lower level than (that is, internal to) those of the pigment cells. If the long cells with the fibres are, on the other hand, considered

the visual cells of Schewiakoff, then again we find nonconformity to a spindle-shaped type, and nuclei not always at a lower level. The matter of alternation of nuclei at different levels seems to me any way too slight a distinction upon which to base a difference in function. It is a necessary mechanical consequence of the crowding together of many cells on one surface. And in many cases in perfectly radial sections through the retina I find the nuclei fewer in number and arranged in very nearly a single level. The retina of the smaller eye represented in Fig. 69 shows this. In sections further along in the same series the nuclei are found at different levels, due without doubt to the slanting cut.



[Dr. Conant did not complete Fig. 72, and the accompanying outline of Fig. 7 of Schewiakoff's memoir (Beiträge zur Kenntnis des Acalephenauges, Morph. Jahrb., Bd. XV, H. 1) has been substituted.—Editor.]

Explanation of Letters in Text Figure.—*C*—concretion cavity; *CO*—cornea; *CP*—capsule of lens; *CSC*—cavity of sensory club; *EC*—ectoderm; *EN*—endoderm; *ENC*—endoderm of sensory club; *L*—lens; *NC*—network cells; *NF*—nerve fibres; *RT*—retina; *SLA*—supporting lamella; *VF*—vitreous body.

Fig. 72 is a horizontal section through the large eye, and shows that here, too, when the sections pass through the eye just radially, the

nuclei are not found at different levels sufficiently definite to suggest two kinds of cells.

In the inner corner of the retina in the same figure (69) are seen cells without pigment which show nuclei undoubtedly at different levels. These cells in this position are a regular feature in the retina of the smaller eye. Schewiakoff considers them purely visual, because of the lack of pigment. In so doing it seems to me he forgets his own standard for discriminating beween pigment and visual cells. The pigment cells of the retina, according to him, are the same thing as the cone-shaped supporting cells found elsewhere in the nervous epithelium, and are, therefore, distinguished from the visual cells primarily by shape and by position of nucleus, secondarily by the greater development of pigment. When on the ground of pigmentation alone he calls the cells in the corner of the retina visual, he judges them by only the second test, and in so doing virtually admits, as it seems to me, that shape of cell and position of nucleus are matters of no great moment. His own standards place him in a dilemma. If on the other hand he judges by the lack of pigment, the cells are visual; if by shape of cell and position of nucleus, they are both visual and pigment cells without the pigment or supporting cells. What use there would be for simple unpigmented cells in one limited region of the retina is hard to see, so he naturally takes the other horn of the dilemma and calls them visual because they have little or no pigment.

The distinction, then, between pigment and visual cells is brought down to one of pigmentation only. Schewiakoff's test for this is that in the visual cells "Das Pigment durchsetzt aber nicht das ganze Protoplasma des centralen Zellenabschnittes, sondern ist auf seine Oberfläche beschrankt (Fig. 19, *sz*), so dass der innere, axiale, stark lichtbrechende Theil vollkommen frei von demselben ist." ('89, p. 37.) That is, in a section through the ends of the retinal cells each pigment cell will appear as a uniformly pigmented area, while each visual cell will appear as a light, strongly refracting spot with a ring of pigment around its periphery. This is the arrangement given in his Fig. 19.

An arrangement so definite ought to be easily made out in sections, yet I have not been able to find it so. My sections show considerable difference in the amount of pigmentation even in material preserved with the same killing agent. If the retina is heavily pigmented the ends of the cells have the appearance shown in Fig. 62, which represents a portion of a cross-section. The ends are seen as clearly defined

polygonal areas differing among themselves in size, but not showing two types of size, or two kinds of pigmentation, the one uniform, the other a ring of pigment around a highly refracting central portion. If the retina is but slightly pigmented—and some were so light as to make depigmentation unnecessary—a difference is seen in the pigment, as shown in Fig. 63, but in no case were areas found that showed a highly refracting centre surrounded by a ring of pigment. (The unexplained structures in Fig. 63 will be referred to a little later.)

Figures 59–62 are a series of four successive sections drawn with the camera lucida for comparison with Schewiakoff's Figs. 20 and 19, and to show that the presence of two types of cells plainly marked within the retina by the position of the nuclei at different levels is at least not clearly demonstrated. Only the nuclei are drawn, since the cell bodies are not easily distinguished from the surrounding fibres. The eye is the same as that from which Fig. 72 was made. Fig. 59 shows a relatively small number of nuclei of slightly larger size than usual. These I take for two reasons to be nuclei of the ganglion cells that are found in the fibres at the base of the retinal cells (Figs. 58, *gc*, 69 and 72). They are the first nuclei struck in tracing sections toward the retina, and in the series from which Fig. 58 was taken similar nuclei appeared in both transverse and radial cuts through the retina stained brightly and clearly with hæmatoxylin, whereas the nuclei of the retinal cells proper were stained a diffuse brownish-yellow from pigment that had evidently gone into solution. Fig. 60 shows the closely aggregated, smaller nuclei of the retinal cells surrounded by the nuclei of the outlying ganglion cells. Schewiakoff's corresponding drawing ('89, Fig. 20) shows at this level a definite alternation of the bodies and nuclei of unpigmented visual cells, with the smaller, pigmented, proximal processes of the pigment cells. In the next section (Fig. 61) the pigmented ends of a few of the cells have been struck, and the following section (Fig. 62) shows that, in this heavily pigmented specimen at least, there is no good evidence within the retina itself of two kinds of cells, so that it is apparent that at any rate we cannot accept Schewiakoff's conception of the structure.

(b) Yet the fibres that Schewiakoff observed and associated with special visual cells occur beyond question. Fig. 64 is a drawing of the first cut through the vitreous body of Charybdea, and in among the sections of the pigment streaks are seen sections of processes lying within clear spaces exactly as Schewiakoff figures his visual fibres ('89, Taf. II, Fig. 18). That the fibres occur is indisputable, but as to the cells

to which they belong I can say nothing except that from such evidence as I have given in the preceding paragraph I conclude that they come from pigmented retinal cells of not very different type within the retina from the others, if different at all.

(c) On the third point, that the pigment streaks in the vitreous body belong to underlying cells and are continued distally into fibrous processes like the visual fibres of Schewiakoff, the evidence is decisive. Fig. 58 has already shown it, and if this were not enough, a case of unusual stoutness of the fibres drawn in Fig. 67 is conclusive. The preparation from which the section is taken was one preserved with corrosive-acetic, and I have drawn the outlines with the camera in order to avoid exaggeration of the fibres as far as possible, and also to show the shrinkage of the vitreous body (*vb*). It is the shrinkage of the vitreous body that makes it so difficult to determine the exact relation of structures seen in the vitreous body to the retina. The fibrous processes run through the vitreous body to the "capsule" of the lens (*cp*) (see also Fig. 72), a layer of homogeneous substance much resembling that of the vitreous body, which is classed as a part of the vitreous body, but usually in the shrinking adheres to the lens. The capsule is therefore regarded by Schewiakoff as a secretion of the lens cells. Some fibres were found by him to have the appearance of branching upon reaching the surface of the capsule, others of passing through it and of seemingly ending among the cells of the lens. The same appearances were given in my sections. It is altogether impossible in the distal portion of the vitreous body to distinguish between the fibres of Schewiakoff and those that come from the long pigment cells. (Figs. 64–66 represent the appearance of the vitreous body at successive levels, and are from the same series of sections as Figs. 59–62 and 72.) In Fig. 64 the sections of the processes that Schewiakoff calls visual are easily distinguished from the sections of the long pigment cells. In Fig. 65, which is two or three sections nearer the lens, the pigment cells are shown by their cross-sections to be tapering down, and in Fig. 66, nearer still to the lens, the two kinds of processes are no longer to be distinguished from each other. In a few cases I have found pigment in a fibre which but for this would be called one of the visual fibres of Schewiakoff. Such considerations as these, the similar appearance in cross-section, the finding of pigment in a few cases, and the inability to trace to any readily distinguished special type of retinal cell, make me wonder whether the visual fibres of Schewiakoff are anything more than the distal processes of pigment

cells, into which the pigment granules happened not to be produced at the moment of fixation.

Fig. 63, however, where the retina was only slightly pigmented, rather speaks against this view, for the number of darkly pigmented areas seen here (which are shown beyond question by radial sections to belong to the long pigment cells) is not great enough to account for the number of both pigment areas and visual fibres of Schewiakoff seen in such a section as Fig. 64. This would throw the visual fibres of Schewiakoff back upon some of the slightly pigmented cells of Fig. 63, otherwise not distinguished. I think the question cannot be settled without the maceration of fresh material, and experiments upon eyes killed in the light and in the dark.

In such cases as that of Fig. 63 it would seem conclusively shown that the long pigment cells must belong to a different type from the short, but as I have already said I can find no regularity in either their shape or in the position of their nuclei. And on the other hand Fig. 58 shows that the reverse relation may obtain and the long cells be less deeply pigmented on the edge of the retina than their shorter neighbors, so that it looks as if all the short cells had to do was to project half their pigment out into the vitreous body in order to become exactly like the long ones. This they could do if, as is possibly the case, they are prolonged into "visual fibres" of Schewiakoff that have escaped observation and so do not appear in the drawing.

Fig. 58 shows one more thing that is worthy of remark in passing. In the preparation in which the vitreous body (at this point at any rate) was not shrunken away from the retina, the fibre from each long pigment cell does not lie in a clearly defined space or "canal," such as is usually described as a constant structure of the vitreous body. Very likely these canals are formed only by shrinkage around the fibres, and the irregular shape of the spaces around the three fibres in Fig. 67 rather bears out the same supposition.

As to the structure of the vitreous body, apart from the fibres and pigment streaks already mentioned, I find it to be made up of prisms extending from retina to capsule of lens, each containing a central axis or fibre. Fig. 64 shows that the space around the pigment areas and "visual fibres," instead of being homogeneous, is wholly filled with the polygonal cross-sections of these prisms. In Charybdea they are generally more difficult to perceive than in my best material of Tripedalia which was killed in acetic acid. In this the polygonal areas stood apart

from each other more plainly. Curiously enough I have been unable to demonstrate in Tripedalia the "visual fibres" of Schewiakoff. Here and there were found spaces that at first sight reminded of them (Fig. 68, *sh*), but they contained no central fibre, and were probably due to shrinkage. The polygonal areas themselves, however, often contained a clear spot in the centre, at one side of which would be found the cross-section of the fibre, as is shown in many cases in Fig. 68. The clear spot is here undoubtedly due to shrinkage of the gelatinous substance of the prism.

I think that these prisms and fibres are the direct continuations of retinal cells. In a section such as that drawn in Fig. 63, which takes just the very tops of the cells of a slightly pigmented retina, in the centre of the section just grazing the space that lies between the retina and the shrunken vitreous body, most of the cells toward the middle (where especially the extreme tips are taken) show in their centres a dot exactly corresponding to the dots in the polygonal areas of the vitreous body. In the exact middle of the section, where only the cell walls appear, slightly indicated, a dot is seen in each case. The size and shape of the ends of the cells correspond with those of the polygonal areas in the vitreous body, and I do not doubt that the latter are continuations of the former. The vitreous body, then, instead of being homogeneous, is composed of the clear highly refracting outer ends of retinal cells. The assumption lies near that these are the true visual rods, but of course it is assumption only.

To give a brief review, the points in which my conclusions differ from those of Schewiakoff are as follows: I find (1) that the long pigment streaks are parts of retinal cells continued into processes like his visual rods; (2) that the vitreous body is composed of prisms with central fibres proceeding from retinal cells; (3) that I am unable to get satisfactory evidence of two types of cell distinguishable within the retina, and at any rate find considerable evidence against the two types he distinguishes.

These results are not wholly satisfactory, for they leave us with three kinds of fibrous processes in the vitreous body which for the present we are unable to trace to three, or even two distinguishable types of cell in the retina. It would be more pleasing if we could confirm Schewiakoff's simple conception of the structure, with its one set of visual rods in the vitreous body referable to a clearly marked type of sensory cells in the retina, but I think the evidence that has been brought up justifies the conclusion that in some respects he saw too much, in

other respects too little. This is not to be wondered at, since his material, to judge from a single statement, consisted of but twelve marginal bodies, and, moreover, the work on Charybdea forms but one portion of a paper that is excellent for the clearness of its descriptions and illustrations.

Before leaving the subject I must mention that Wilson suggested from his observations on Chiropsalmus that the vitreous body had a prismatic structure, but he was probably mistaken when he thought he found evidence of nuclei in it. Claus says that the retina is composed of pigment and rod cells alternating, and Wilson agrees with him, but under a sketch of a sense cell from the nerve he makes the express statement "not very well preserved." It seems very probable, therefore, that he followed Claus's interpretation rather than independent observations, and Claus interpreted his results very much by analogy of what had been found in other forms.

The smaller complex eye which is represented in Fig. 69 agrees in structure very closely with the larger. The chief differences are that sections do not show pigment extending into the vitreous body, that there is no "capsule" to the lens, and that the lens seems to be supported by a kind of stalk formed by a thickening of gelatine of the supporting lamella (*sl*). The gelatinous thickening lies between the lens and an outgrowth of endodermal cells (*en*) from the canal of the club. This outgrowth is a constant feature, figured by Claus and Schewiakoff for Charybdea, and by Wilson for Chiropsalmus, and found in Tripedalia also. The regularity of its appearance in all three genera leads one to suspect that it may have some significance not yet understood.

Just above the smaller eye there lies a mass of cells of peculiar structure (Fig. 69, *nc*). They are of a rounded polygonal contour, with a comparatively small circular nucleus in the centre, and are found in this region only. In and amongst them bundles of fibrous tissue are found in the sections, which pass from the surface cells to the supporting lamella. Claus describes the contents of these cells as coarsely granular protoplasm and says they cannot be taken for ganglion cells. He is inclined to believe that they play the part of a special supporting tissue. Schewiakoff, on the other hand, is convinced that they are ganglion cells, and finds processes passing out from them ('89, Taf. II, Fig. 22). I find, however, that the cell contours are perfectly regular and clearly without processes, and it is incomprehensible to me how, if his material was at all well preserved, he could for a moment have taken them for the same

thing as the big multipolar ganglion cells with large nucleus and nucleolus which lie in about the same region and were correctly described and figured by Claus but are not specially mentioned by Schewiakoff. I cannot agree with Claus, however, that their contents are composed of coarsely granular protoplasm. That which appears such by low magnification shows itself under high powers to be a beautiful network with thickenings at the nodes of the meshes, which is brought out very plainly by a cytoplasmic stain such as Lyons blue. Around the nucleus is seen a more or less well-defined clear zone. What the function of the cell is remains as unknown to me as to Claus and Schewiakoff.

There is left one more point in reference to the nervous system upon which I wish to say a word. Claus and Schewiakoff both describe the wall of the crystalline sac as structureless, formed by the bare supporting lamella. The credit is due to H. V. Wilson of finding in Chiropsalmus that it has a special lining of epithelial cells, which he figures as a continuous, flattened layer. In both Charybdea and Tripedalia I find traces of the same in nuclei here and there, but whether they are the remains of a once continuous layer or not the sections do not show satisfactorily.

This ends the account of what it seemed worth while to say at present upon the nervous system. In concluding, the writer wishes to express his thanks for the help afforded by Dr. Wilson's notes, in particular on the subject of the vascular lamellæ, and desires to make especial acknowledgment of his indebtedness to Professor Brooks, whose suggestions, based upon many years of experience with the Medusæ, have been most welcome and helpful, and whose evidences of unfailing kindliness, both in Jamaica at the time the material was obtained and in Baltimore when it was being studied in the laboratory, take a most honored part in the pleasant memories associated with the work.

LITERATURE REFERRED TO.

Clarke, H. J. '78. Lucernariæ and their Allies. Washington: Smithsonian Institution.

Claus, C. '78. Ueber Charybdea marsupialis. Arb. aus d. Zool. Inst. d. Univ. Wien, Band II, Heft 2.

Doflein, F. '96. Die Eibildung bei Tubularia. Zeitsch. f. wiss. Zool., Bd. LXII, Heft 1.

Haeckel, E. '79. Das System der Medusen. Jena.—'81. Challenger Report on the Deep-sea Medusæ. Vol. IV.

HERTWIG, O. and R. '78. Das Nervensystem und die Sinnesorgane der Medusen. Leipzig.

HESSE, R. '95. Ueber das Nervensystem und die Sinnesorgane von Rhizostoma Cuvieri. Zeitschr. f. wiss. Zool., Bd. LX, Heft 3.

MÜLLER, F. '59. Zwei neue Quallen von St. Catherina (Brasilien). Abhandlungen der naturf. Gesellschaft zu Halle.

SCHEWIAKOFF, W. '89. Beiträge zur Kenntniss des Acalephenauges. Morph. Jahrb., Bd. XV, Heft 1.

WILSON, H. V. Unpublished notes.

TABLE OF REFERENCE LETTERS.

afr = adradial furrow.
afr' = furrow in Tripedalia that separates perradial from interrad. regions in lower half of bell. (In Charybdea the same furrow is directly continuous with *afr.*)
ax = axis of nerve.
c = concretion.
cc = canal underneath *ivl*, connecting the two adjacent marginal pockets.
ccl = circular canal.
ci = cilia.
cm = circular muscle.
co = cornea.
cp = capsule of lens.
cs = covering scale of niche.
csc = canal of sensory club.
ct = canal of tentacle.
ct' = beginning of canals of lateral tentacles in Tripedalia.
ec = ectoderm.
ece = ectoderm of exumbrella.
ecs = ectoderm of subumbrella.
ed = distal paired eye.
el = larger unpaired eye.
en = endoderm.
enc = endoderm of sensory club.
enf = tract of nerve fibres underlying endoderm.
enfl = endoderm of floor of stomach.
enp = endoderm of stomach pockets.
enr = endoderm of roof of stomach.
ens = endoderm of stomach.
ep = proximal paired eye.
es = smaller unpaired eye.
fc = funnel leading into canal of sensory clubs.
fp = fibre from subepithelial plexus of subumbrella.
fph = filaments of phacellus.
frn = frenulum.
ft = funnel-shaped depression in ectoderm axial to base of tentacle.
g = gelatine.

gc = ganglion cell.
ge = gelatine of exumbrella.
go = gastric ostium.
gs = gelatine of subumbrella.
hvl = horizontal vascular lamella.
i = interradius.
if = interradial funnel of bell cavity.
ifr = interradial furrow.
ivl = interradial vascular lamella.
l = lens.
lv = lip of valve.
m = bell margin.
mc = mucous cell.
mep = mesogonial pocket.
mo = mouth.
mp = marginal pocket.
mp' = smaller marginal pockets, in Tripedalia.
mst = muscle of stock of sensory club.
mt = muscle at base of tentacle.
n = nerve.
nc = network cells, in sensory club.
nf = nerve fibres.
nm = nematocyst.
nst = nerve of stalk of sensory club.
osn = outline of sensory niche.
p = perradius.
pe = pedalium.
ph = phacellus.
pr = proboscis.
r = reproductive organ.
rc = remains of concretion.
rcl = radial canal.
rg = radial ganglion.
rm = radial muscle.
rn = radial nerve.
rns = root of nerve of sensory club.
rs ? = remains of stalk (?) of sensory organ.
rt = retina.
s = stomach.
sc = bell cavity.
scl = sensory club.
scn = supporting cell of nerve.
se = sensory epithelium.
sh = shrinkage space.
sl = stalk of lens.
sla = supporting lamella.
sn = sensory niche.
so = sensory organ in proboscis of Tripedalia.
sp = stomach pocket.
sph = stalk of phacellus.
ss = stalk of sensory organ, in proboscis.
st = stalk of sensory club.

su = suspensorium.
sub = subumbrella.
tl = lateral tentacle.
tm = median tentacle.
v = velarium.
va = vacuole.
vb = vitreous body.
vc = velar canals.
ve = edge of velarium.
vfs = visual fibres, according to Schewiakoff.
vg = valve of gastric ostium.
vl = vascular lamella.
vlc = vascular lamella connecting *vls* with *vlm*.
vlm = vascular lamella of margin.
vls = vascular lamella of sensory niche.
vlst = vascular lamella of sensory niche at base of stalk.
wc = wandering cells.
w–x–y–z = successive levels of Figs. 40–43 on Fig. 5.

DESCRIPTION OF FIGURES.

Fig. 1. Charybdea Xaymacana, from one of the four interradial sides.
Fig. 2. The same from above.
Fig. 3. The same from below, the four tentacles cut off.
Fig. 4. The same cut in halves vertically (or radially) through a perradius.
Fig. 5. The same cut in halves vertically (or radially) through an interradius.
Figs. 6–16. Diagrams of horizontal (or transverse) sections through C. Xaymacana at successive levels.
Fig. 17. Tripedalia cystophora, from one of the four interradial sides.
Fig. 18. The same from below.
Fig. 19. The same cut in halves vertically through a perradius.
Fig. 20. The same cut in halves vertically through interradius.
Figs. 21–30. Diagrams of horizontal sections through T. cystophora at successive levels.

(The following are of Charybdea, except when specially stated otherwise.)

Fig. 31. Horizontal section through the suspensorium.
Fig. 32. Diagram of a gastric ostium seen from the stomach side.
Fig. 33. Diagram of a vertical section through a gastric ostium.
Fig. 34. Diagram of a horizontal section through a gastric ostium.
Fig. 35. Diagram to illustrate the formation of the central and peripheral gastrovascular systems of a Hydromedusa (*a*, *b*, and *c*) and a Cubomedusa (*d*).
Fig. 36. Vertical section through the upper part of the bell, adradial, to show horizontal vascular lamella.
Fig. 37. Vertical section through the perradius, to show vascular lamella of the niche of the margin.
Fig. 38. Vertical section a little to one side of the last, to show same structure.
Fig. 39. Horizontal section through the upper part of the sensory niche, to show vascular lamella of the niche.
Figs. 40–43. Horizontal sections through the base of a pedalium at successive levels, *w–x–y–z*, Fig. 5, to show marginal lamella.

Fig. 44. Diagram to show relations of sensory niche, of bell margin and velarium in adult Tripedalia. The velarium represented as pendant.

Fig. 45. To show the same structure in a young Tripedalia.

Fig. 46. Horizontal section through the last just at the margin, to compare with Fig. 29.

Fig. 47. Cross-section through the nerve ring.

Fig. 48. The structure of the nerve as seen by focusing at successive levels.

Fig. 49. Diagram to show the relation of the nerve ring to the sensory club.

Fig. 50. Horizontal section through the upper part of the sensory niche, to show passage of nerve root through gelatine of subumbrella to stalk of sensory club.

Fig. 51. Vertical section through base of stalk of sensory club, to show same passage.

Fig. 52. Similar section to last, but nearer to perradius, to show sub-endodermal tract of nerve fibres.

Fig. 53. Sensory organ in proboscis of Tripedalia, as seen from surface in living animal.

Figs. 54 and 55. Sections of same sensory organ.

Fig. 56. Vertical section through one side of proboscis, to show sensory organ attached to endoderm. (Tripedalia.)

Fig. 57. Diagram of the outlines of sensory club seen from the side, by camera lucida.

Fig. 58. Part of retina of larger complex eye cut radially.

Figs. 59–62. Four sections in direct sequence through retinal cells transversely, larger eye.

Fig. 63. Transverse section through the tips of cells of a slightly pigmented retina, larger eye.

Figs. 64–66. Three transverse sections through vitreous body at different levels. All from same series, but not in direct sequence ; larger eye.

Fig. 67. Radial section through retina, to show fibres from the long pigment cells ; larger eye.

Fig. 68. Transverse section through vitreous body of Tripedalia near retina.

Fig. 69. Vertical section through smaller complex eye.

Fig. 70. Wandering cells, Charybdea.

Fig. 71. Floating mass, from stomach pocket of Tripedalia.

Fig. 72. Horizontal section through larger complex eye. (See text figure, p. 50.)

Fig. 1.

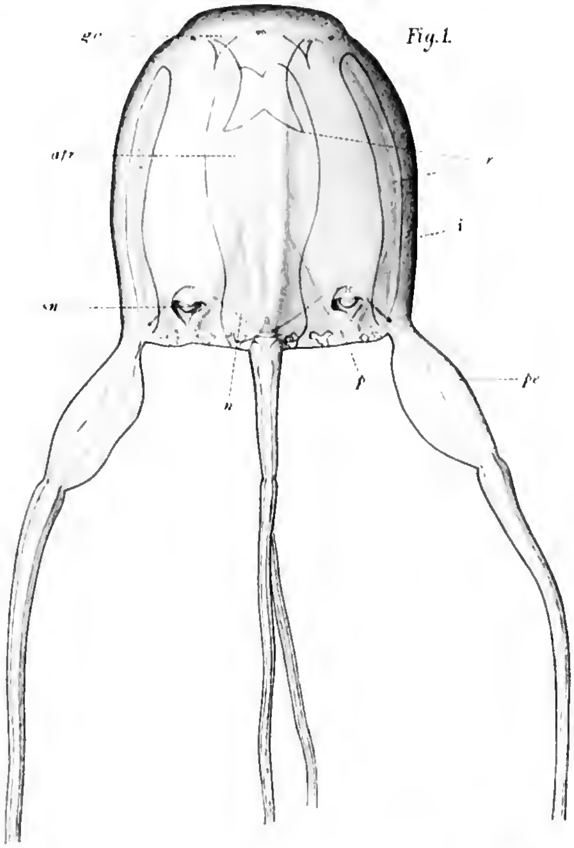
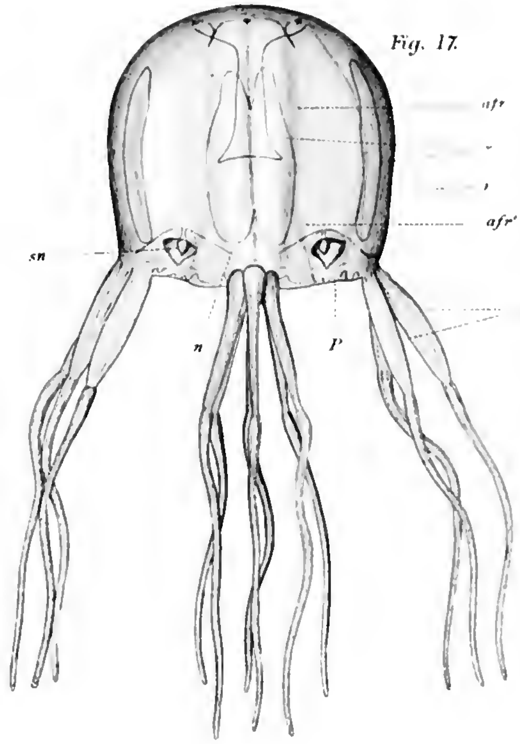


Fig. 17.



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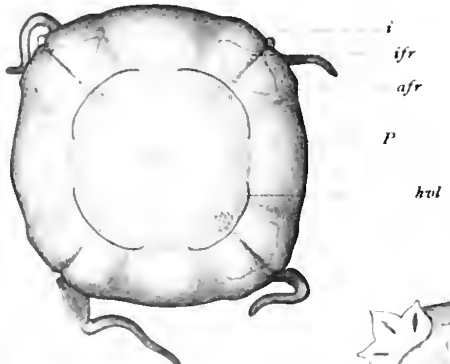

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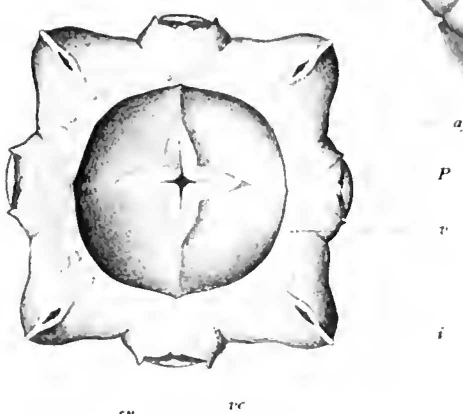

Fig. 18.

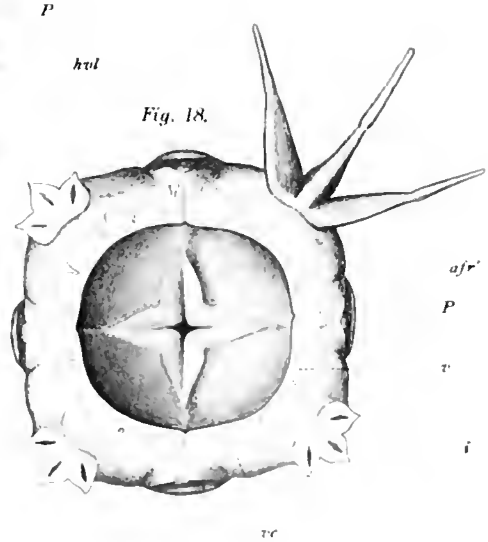

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Fig. 4.

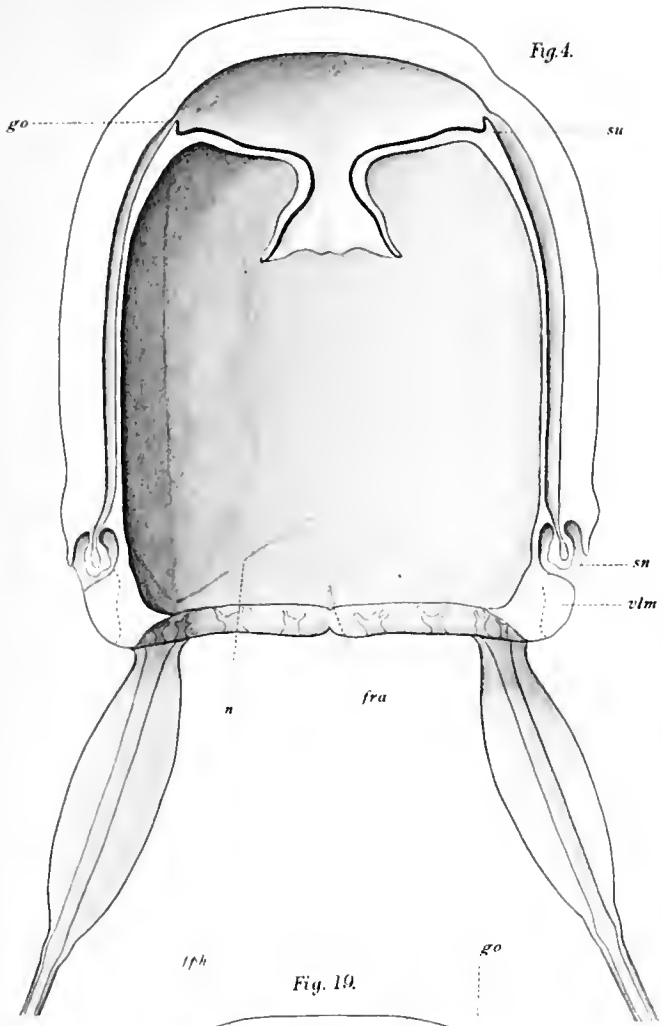


Fig. 5.

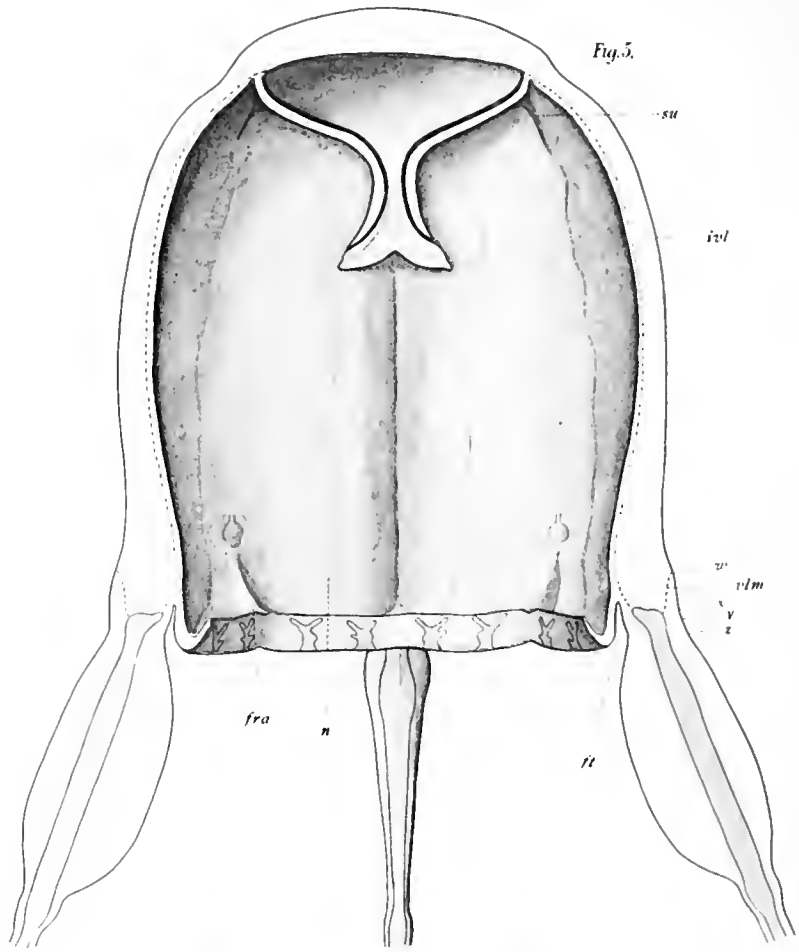


Fig. 19.

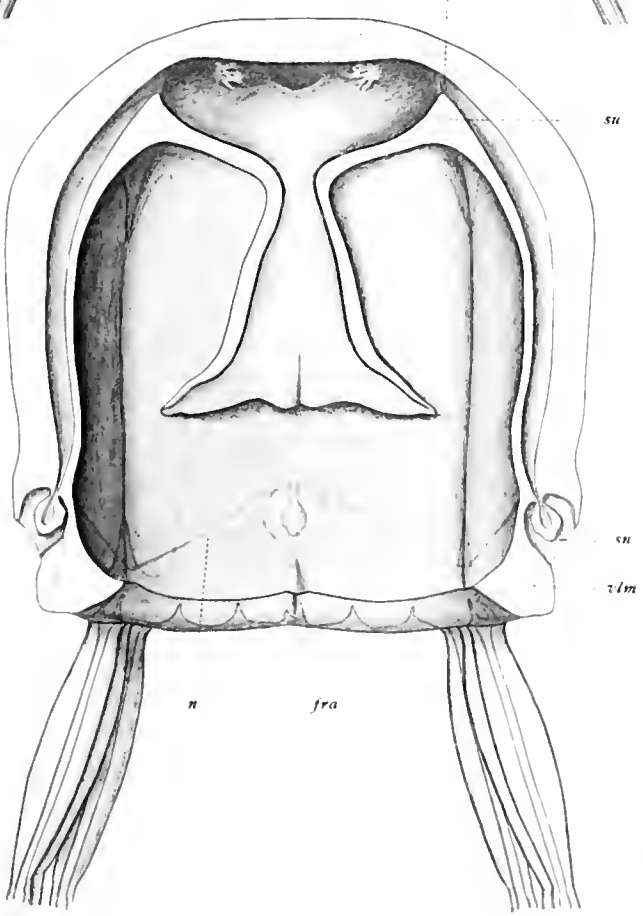


Fig. 20.

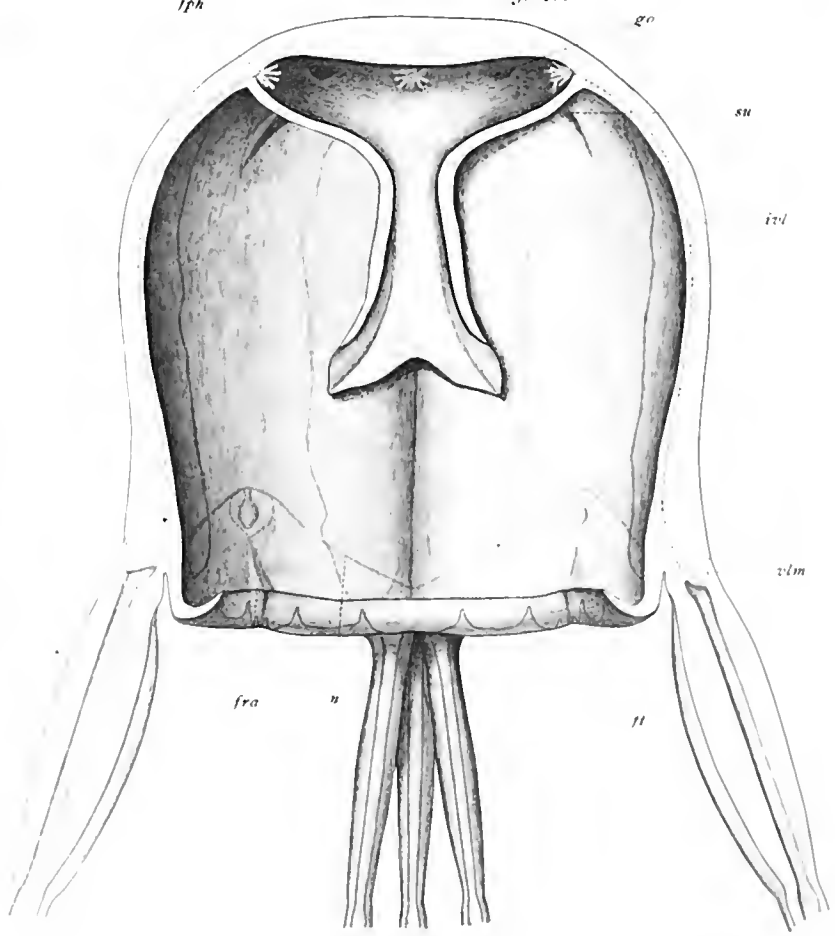
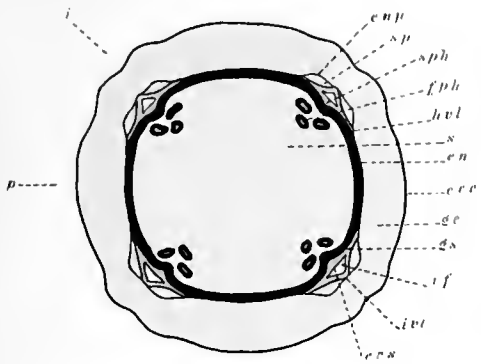


Fig. 6.



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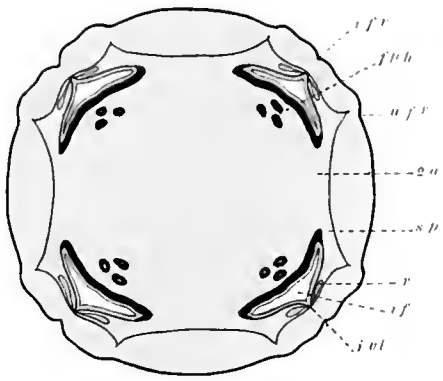

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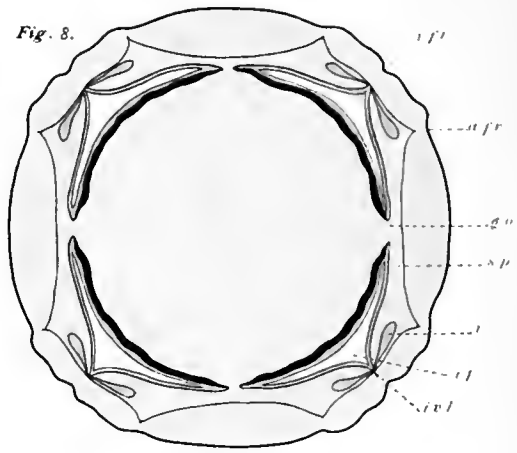


Fig. 9.

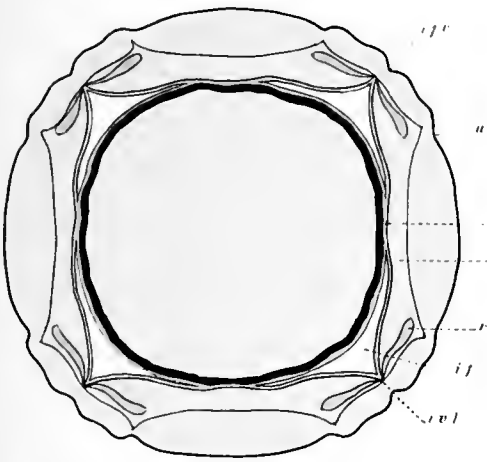


Fig. 10.

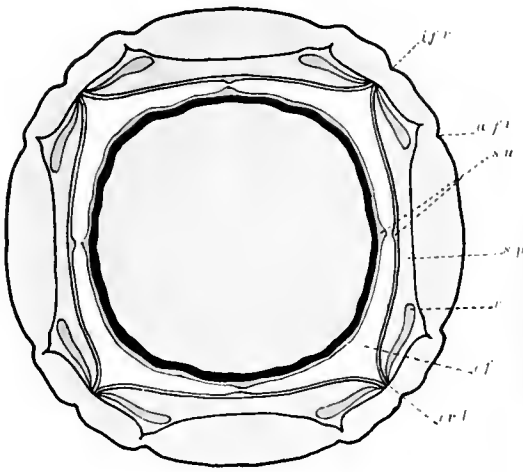


Fig. 11.

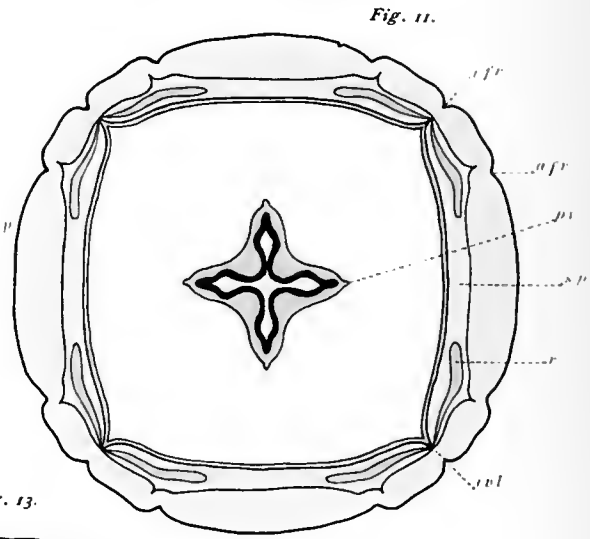


Fig. 12.

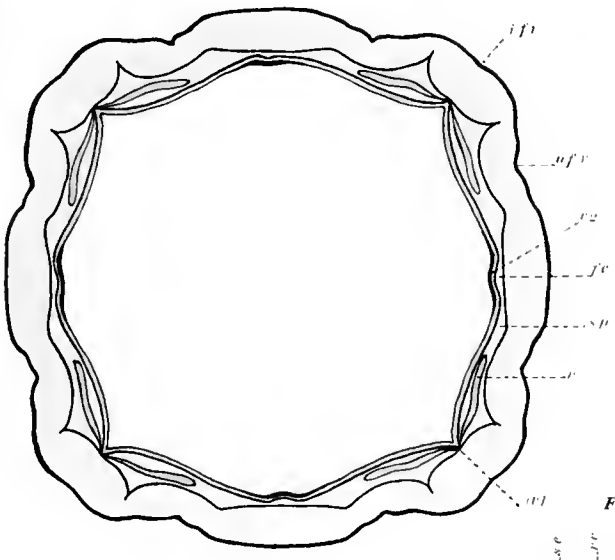
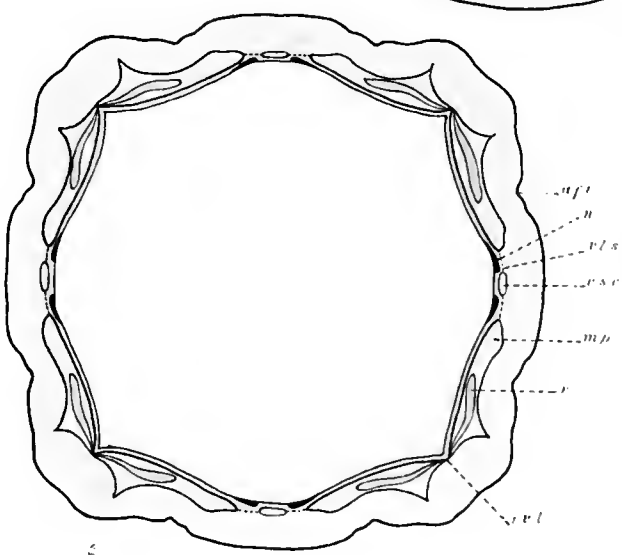


Fig. 13.



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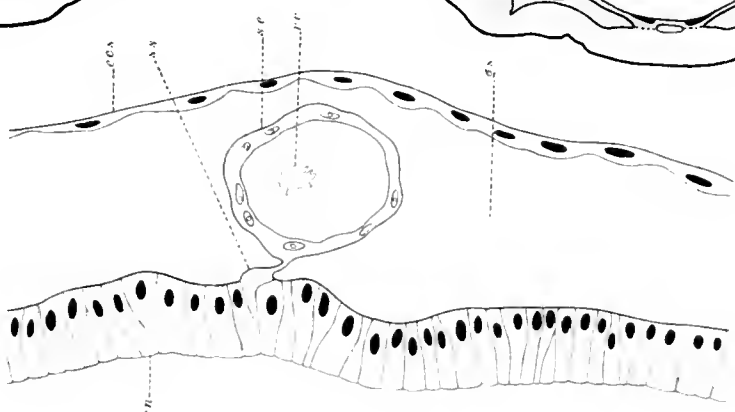

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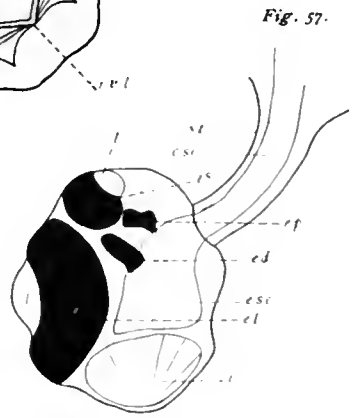

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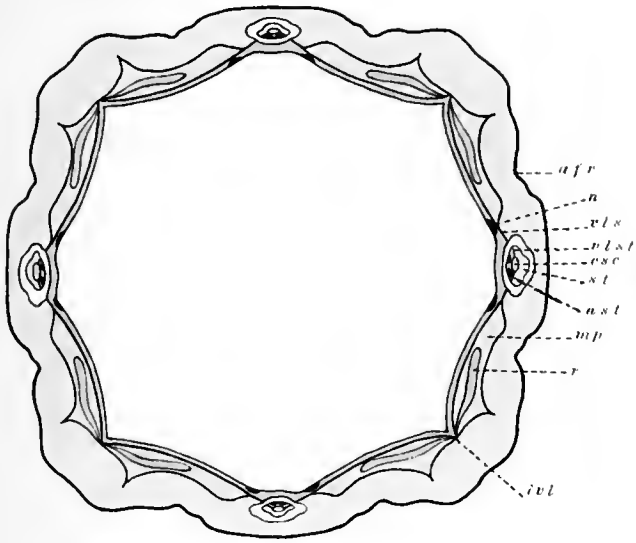

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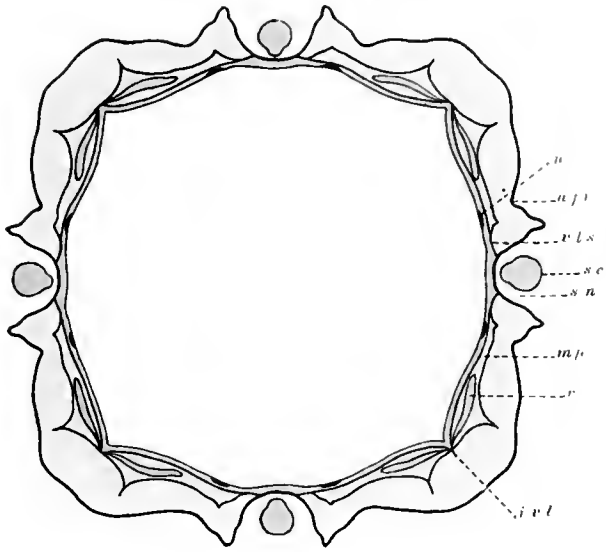

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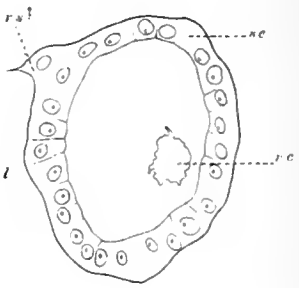

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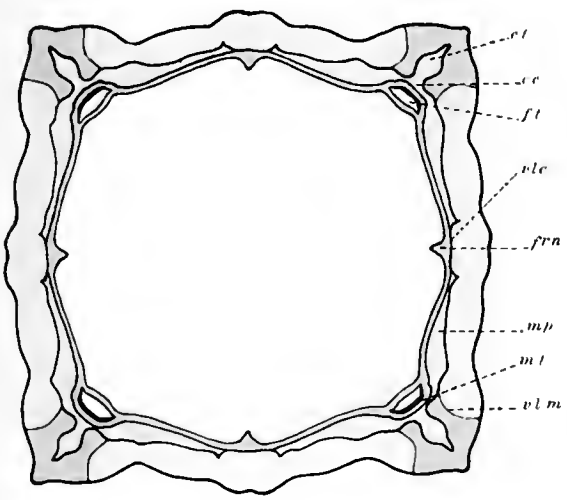

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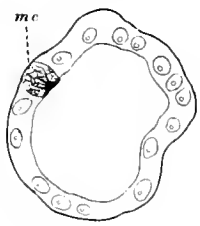

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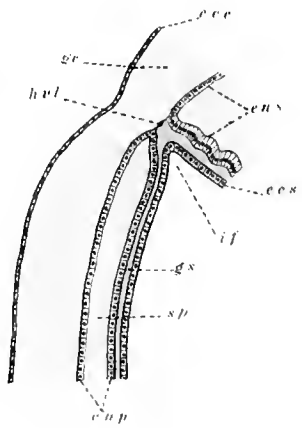

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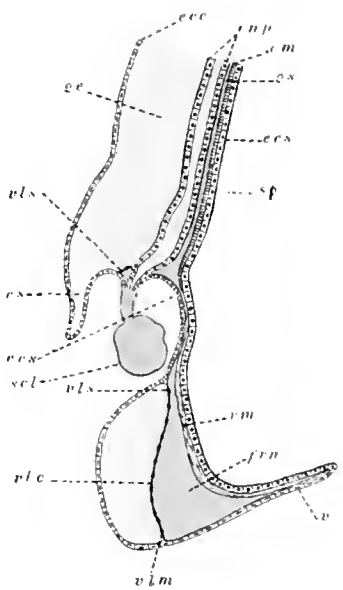

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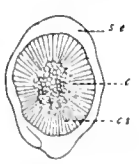

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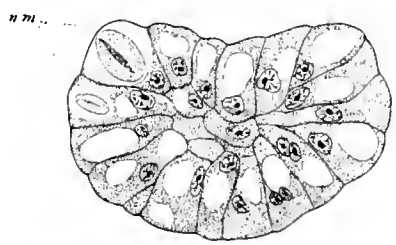

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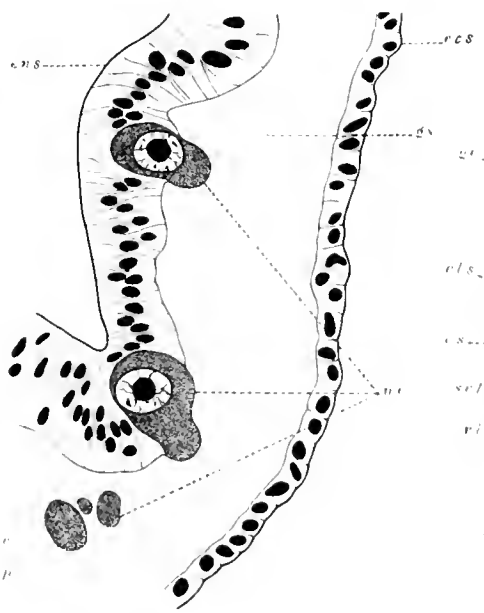

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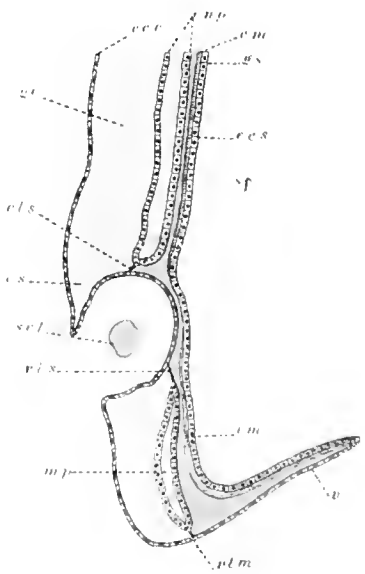

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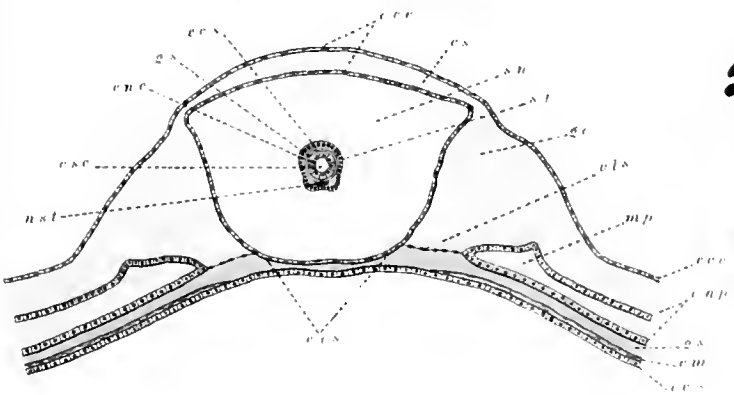

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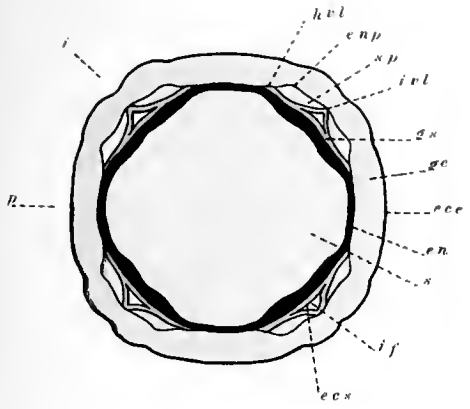

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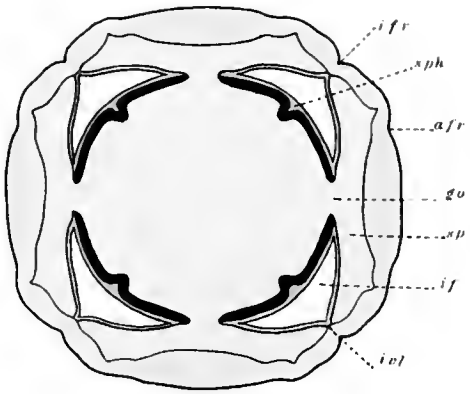

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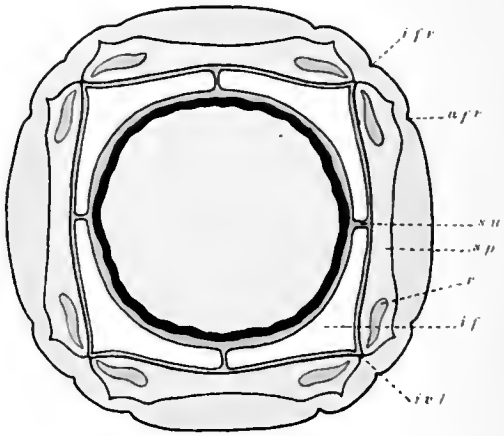

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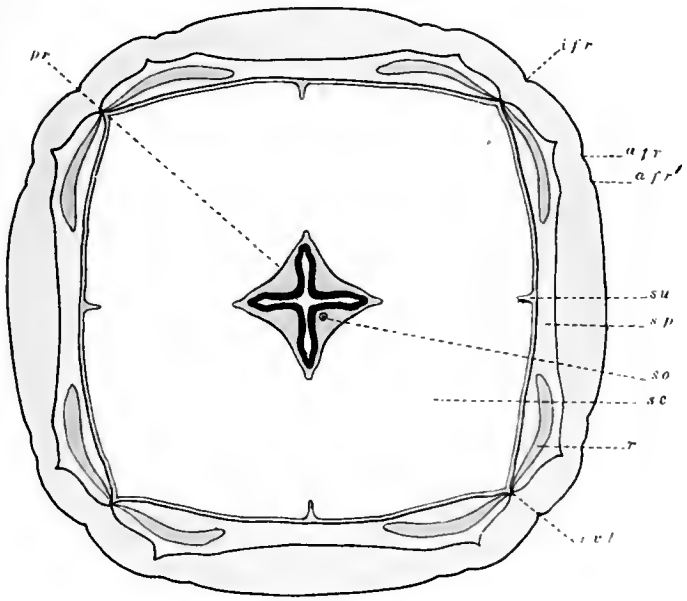

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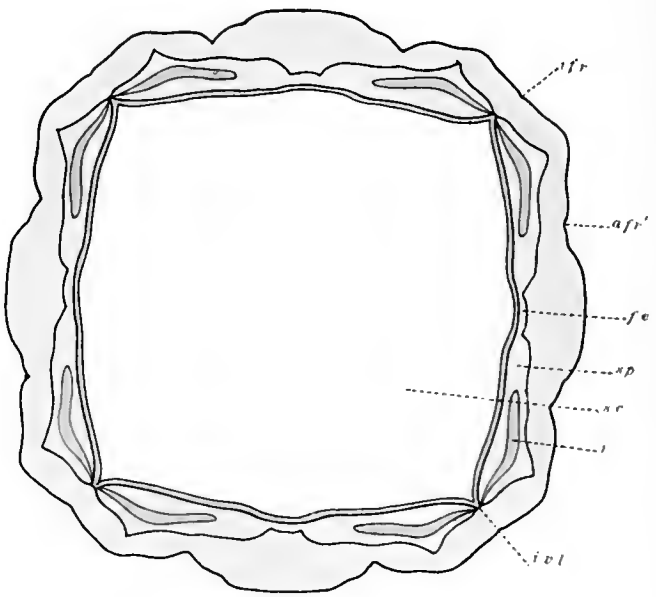

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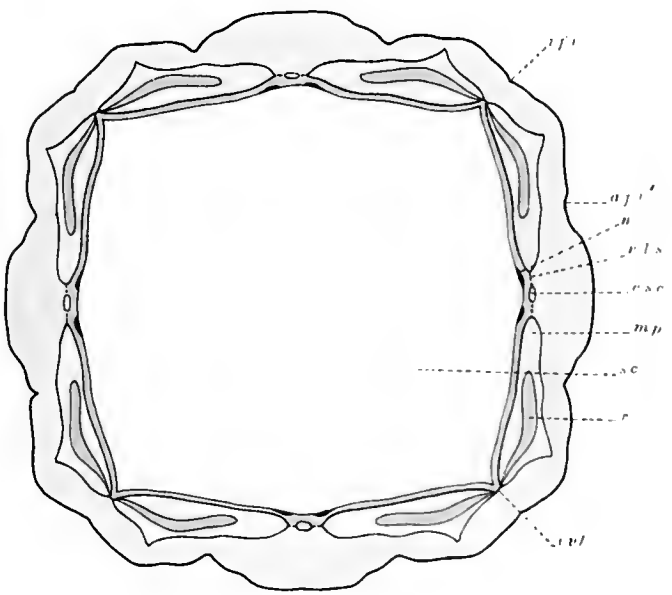

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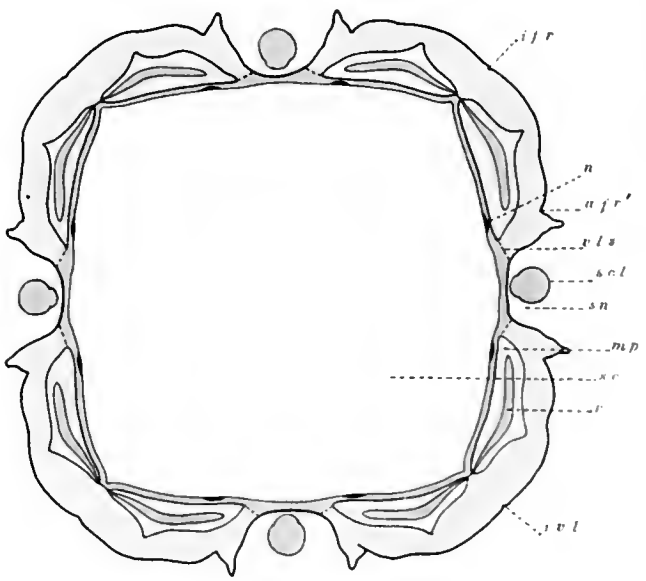

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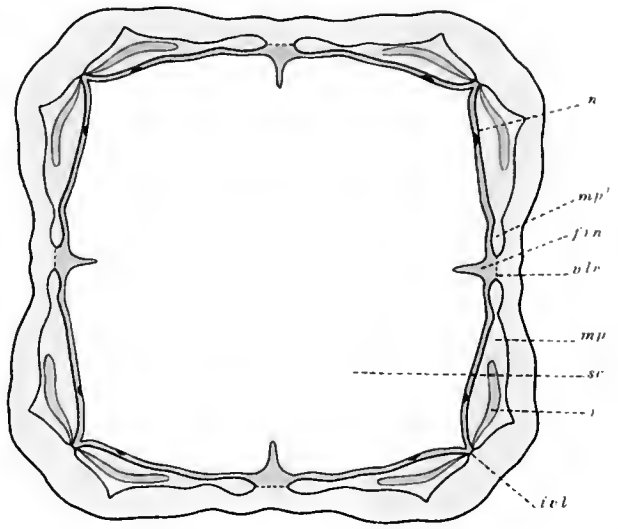

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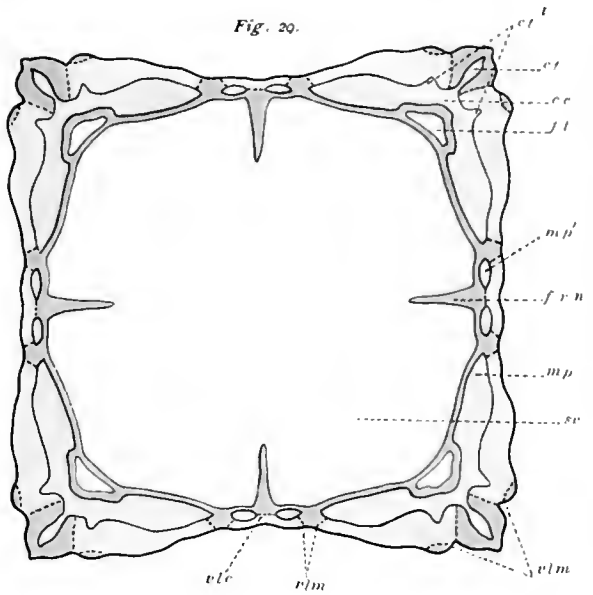

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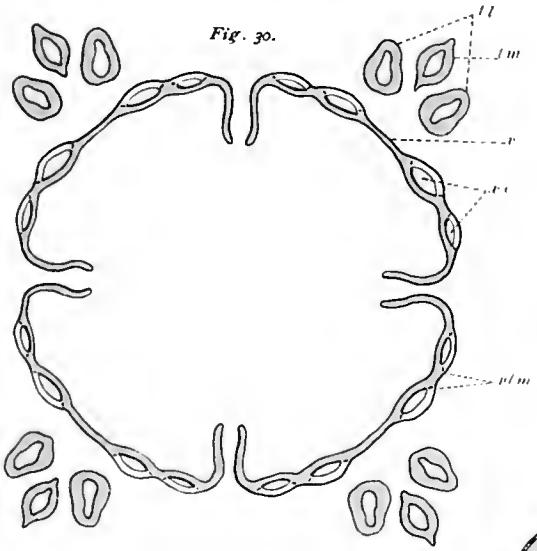

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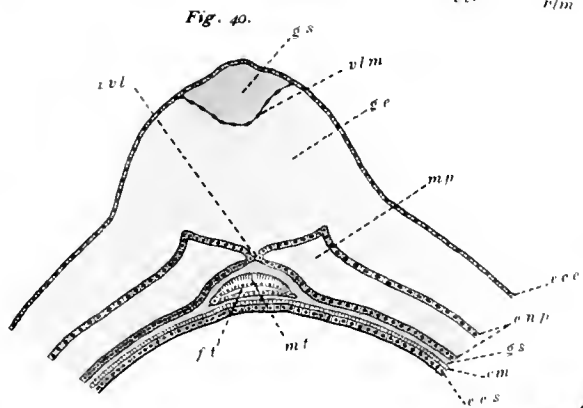

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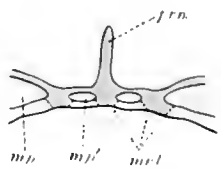

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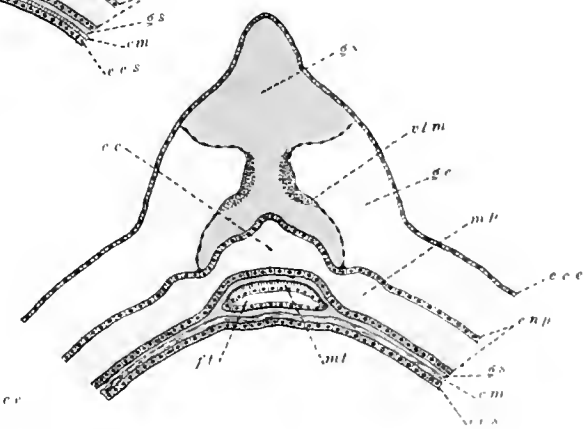

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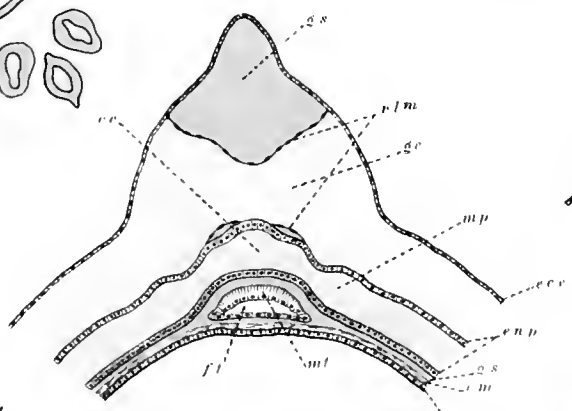

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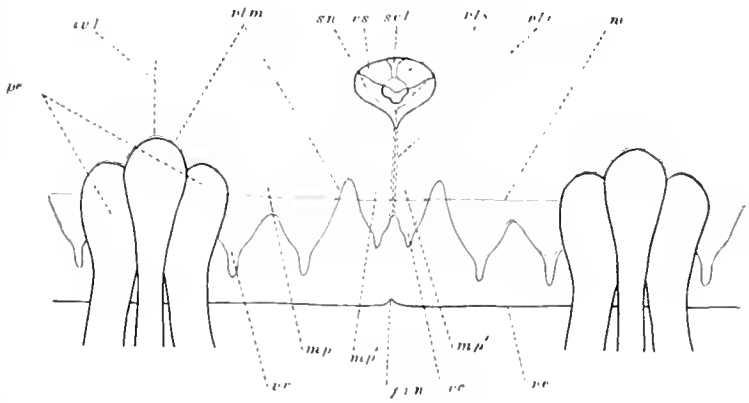

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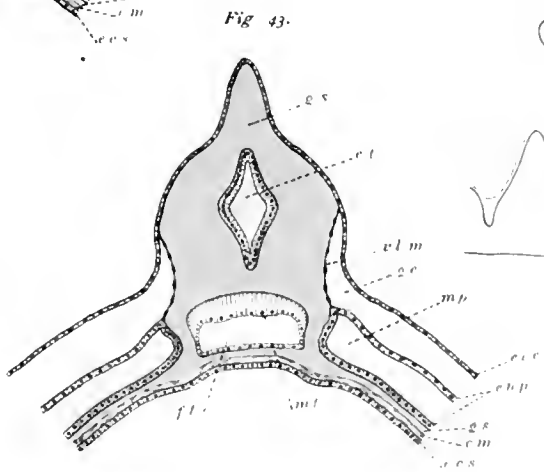

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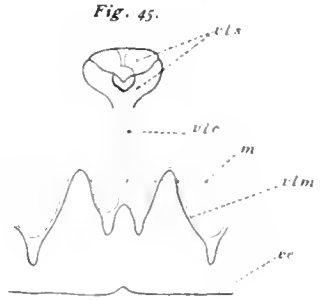

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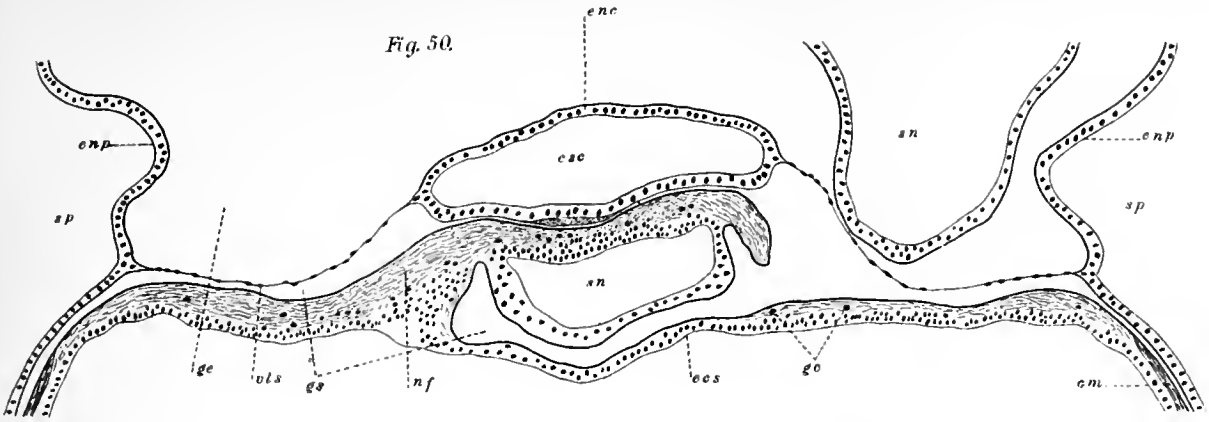

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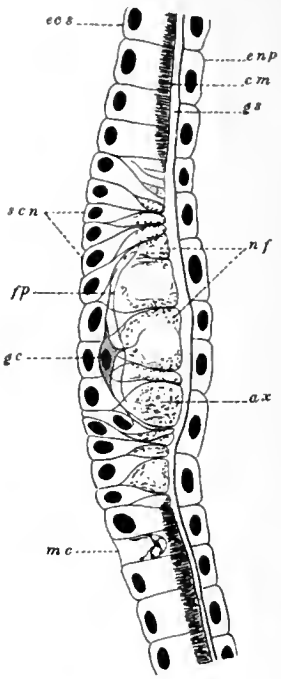

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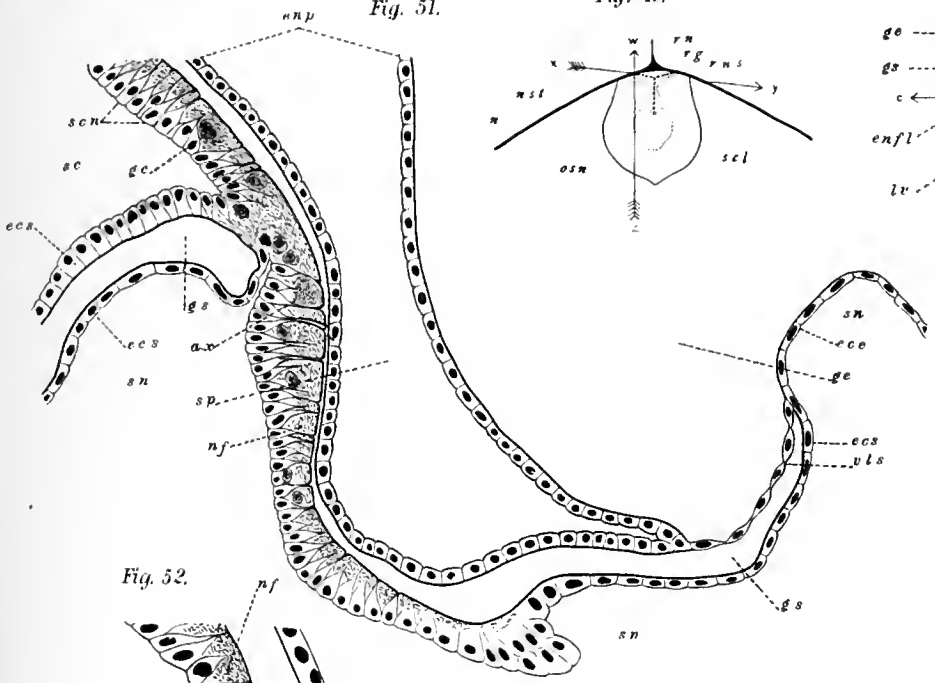
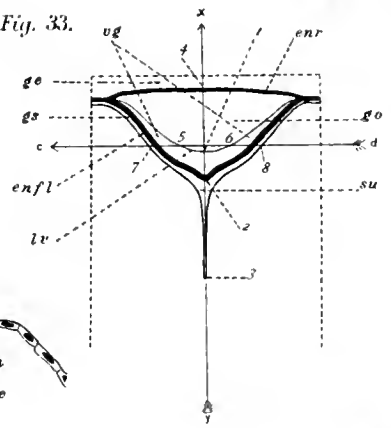


Fig. 49.

Fig. 33.



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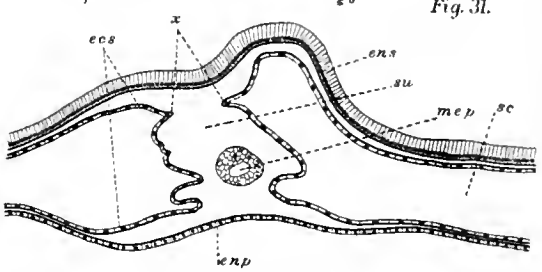

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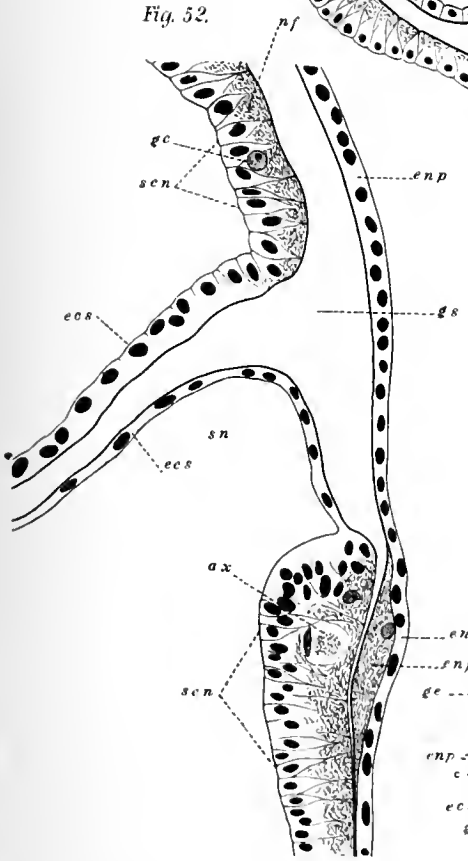

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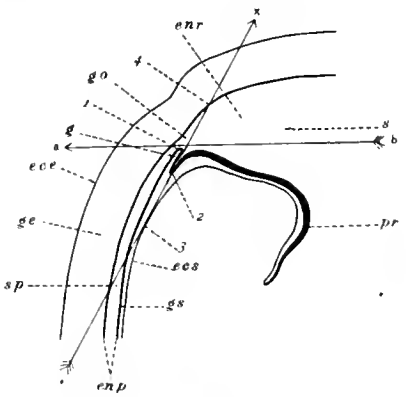

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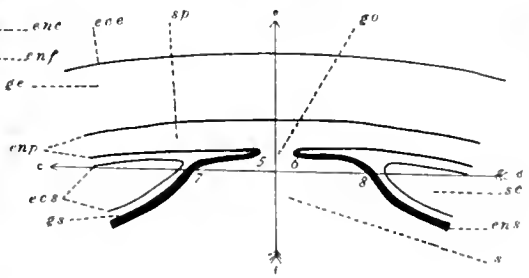

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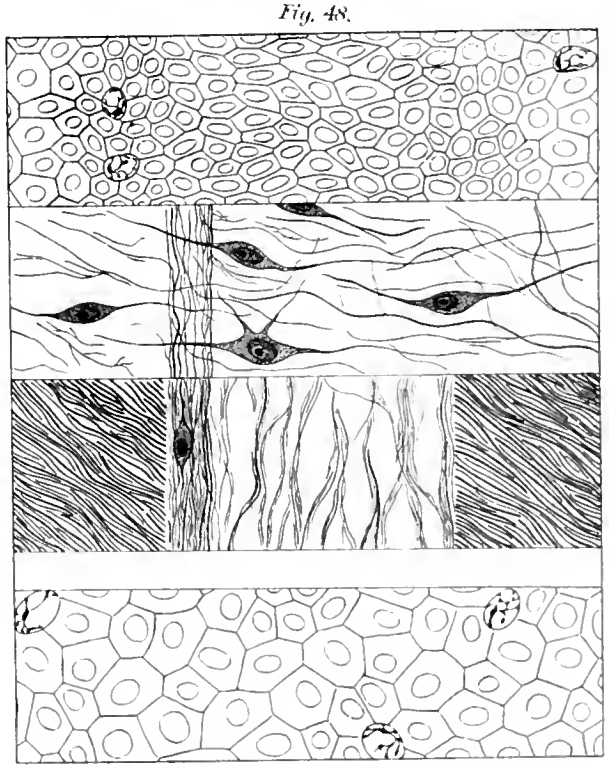

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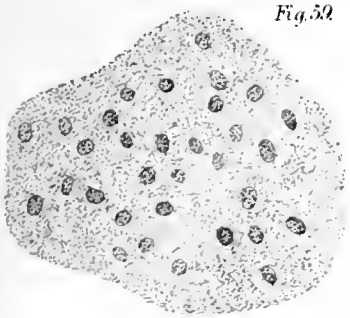

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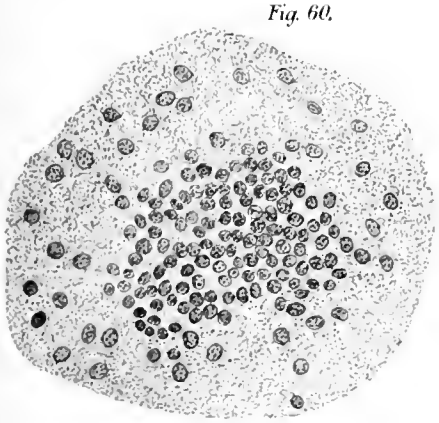

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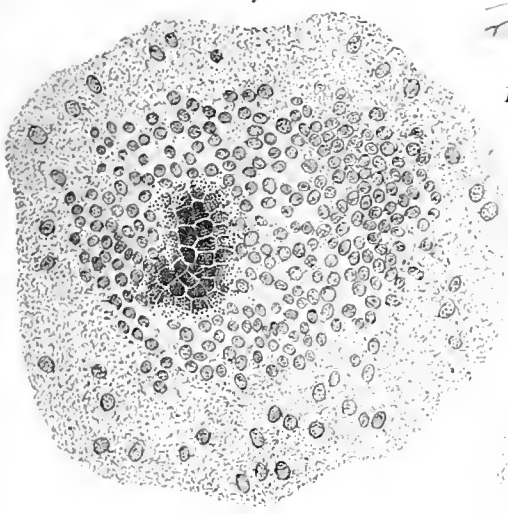

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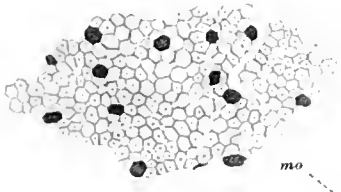

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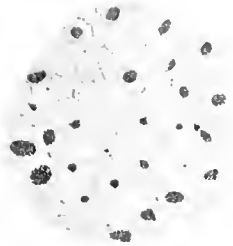

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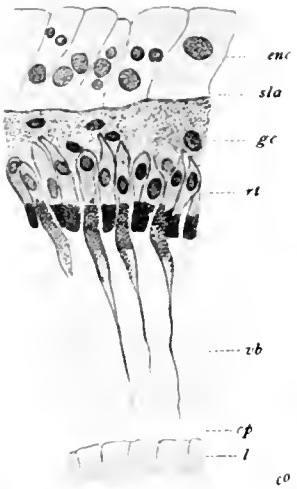

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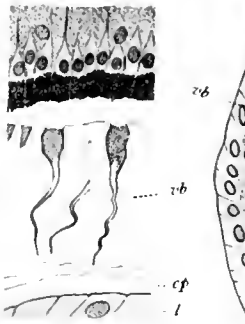

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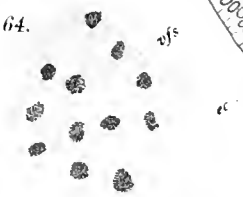

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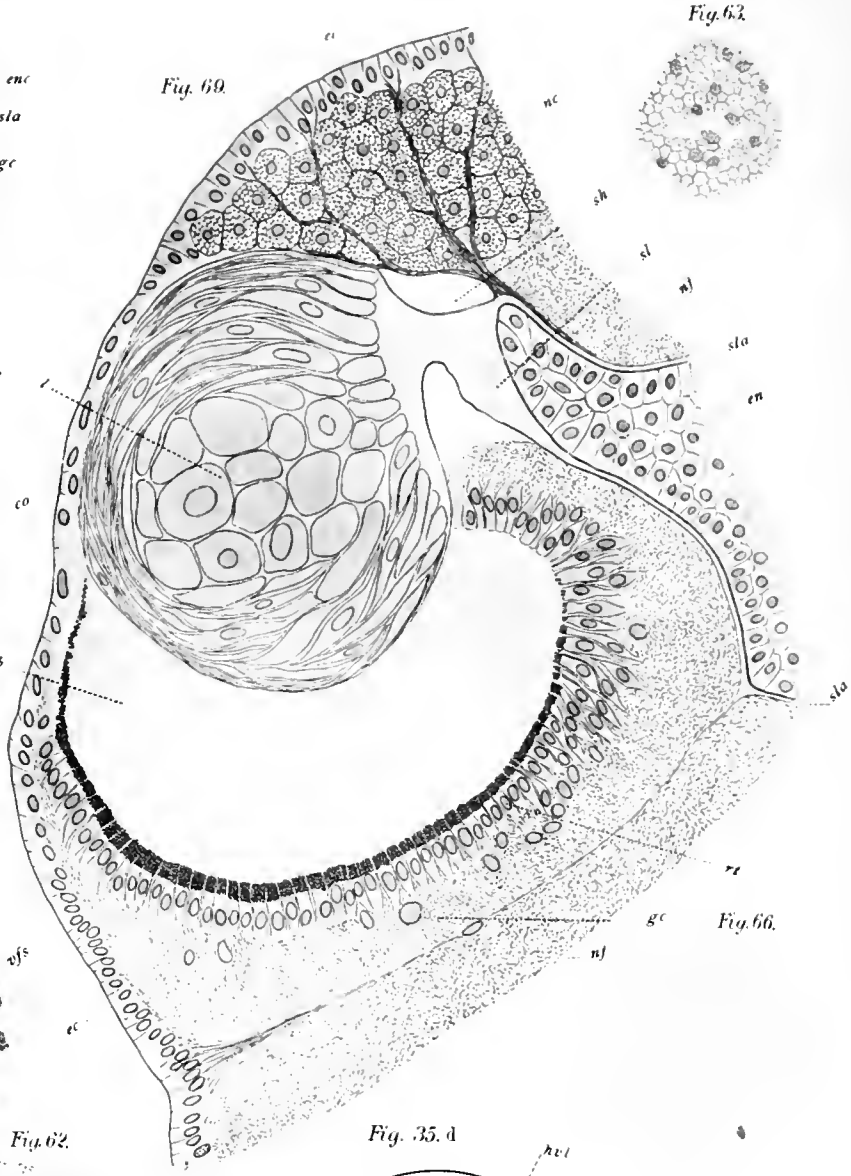
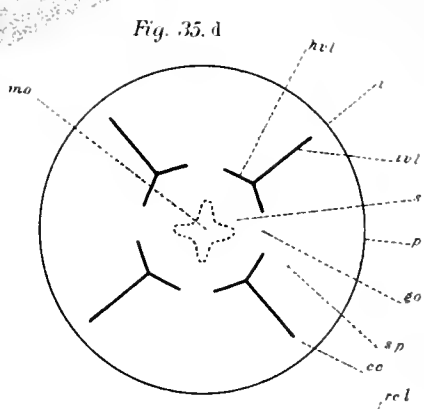


Fig. 63.

Fig. 66.

Fig. 35. d



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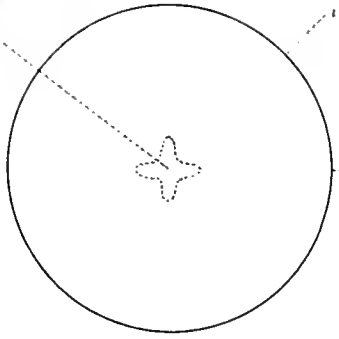

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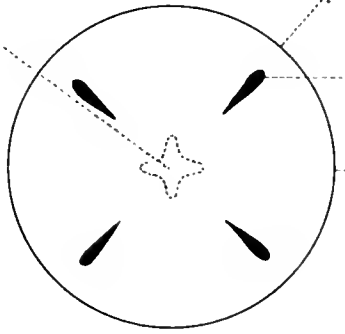

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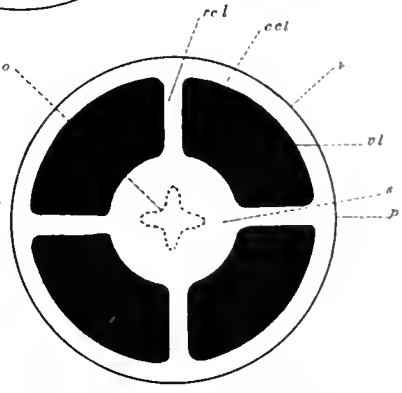

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This Memoir is a continuation of the work upon the Cubomedusæ which was begun by the late Dr. FRANKLIN STORY CONANT, and it contains his notes of physiological experiments, as well as new results which have been obtained by Dr. E. W. BERGER from the study of material which had been collected by Dr. CONANT, who had hoped to make it the object of further study.

In order that this work may be made public as a continuation of Dr. CONANT'S researches, his sister, GRACE WILBUR CONANT, has, with the coöperation of other members of his family, made an adequate and generous provision for its publication.

For this gift, which is at once a contribution to science and a memorial of an able and promising investigator, lately student and fellow in this institution, the Johns Hopkins University returns its grateful acknowledgments.

DANIEL C. GILMAN, *President.*
W. K. BROOKS, *Professor of Zoölogy.*

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HISTOLOGICAL.

INTRODUCTION.

This paper may be regarded as a continuation of the Cubomedusan studies pursued by Dr. F. S. Conant while in Jamaica, in 1896 and 1897, with the Johns Hopkins Marine Laboratory. His systematic and anatomical results have since been published as his Dissertation ("The Cubomedusæ") by this University. Conant described this paper as Part I, hoping soon to add a second part on the physiology and the embryology, for which he had some notes and material at hand. Returning, however, to Jamaica with the laboratory, in 1897, he continued his physiological experiments, and preserved material for histological purposes. Upon the untimely death of Conant, his material and notes were placed in my hands by Professor Brooks, to whom I here take the opportunity of expressing my appreciation and sincere thanks for the honor thus conferred and for the many favors received.

In this paper I shall note at some length Conant's physiological results and append his notes. I shall also add my results on the histology of the eyes and the sensory clubs in general, with some few facts on the histology of the tentacles. The embryology will be reserved for a future paper.

The forms used in the physiological experiments were Charybdea Xaymacana, one of the two species (see Literature V, a and b) first found and described by Conant; Aurelia aurita; Polyclonia and Cassiopœa. The greater number of Conant's notes are on Charybdea, and were left by him just as taken at the time of experimenting. Many of these notes are highly interesting and in the main fit in well with Romanes'[I] and Eimer's[IV] results.

Dr. Conant's work on Charybdea, in 1897, was wholly done at Port Antonio, Jamaica. At first Conant had only varying success in obtaining Charybdea, scouring the harbor and neighboring water at all hours, only to obtain but few specimens. It was on the forenoon of August 7th, while we were dredging at the head of East Harbor with a steam launch, that many Charybdeae were brought up in the dredge. This gave Conant a clue to their whereabouts and to the means of obtaining them, and from that time on he was able to

obtain them in abundance. His first physiological experiments were begun on August 4th and continued thereafter at intervals of several days until his departure from Jamaica on September 6th.

Dr. Conant usually performed his experiments during the second half of the forenoon, after the animals had stood for a few hours in the laboratory.

The building that was rented at Port Antonio for a laboratory had, in the basement, a photographer's dark-room, which was of great service to Conant in his experiments.

The experiments on Aurelia, in 1897, were also performed at Port Antonio, between August 6th and 9th. The experiments on Cassiopœa were probably made at Port Antonio, where specimens were occasionally obtained.

The notes on Aurelia and Polyclonia, in 1896, were taken at Port Henderson, between May 12th and June 27th.

In his notes Conant speaks of Polyclonia and Cassiopœa. It is at present undetermined whether he really had both forms or whether he uses the two names for the same form. It seems likely that in 1896 he thought the form to be Polyclonia, while for some reason, in 1897, he supposed it to be Cassiopœa. I have examined several specimens of these medusæ brought from Port Antonio and find that they all have twelve marginal bodies and twenty-four radial canals, according to which (V, Haeckel's System), they should be Polyclonia. Conant, however, speaks of removing sixteen marginal bodies, which seems to indicate that he had Cassiopœa. A careful classification of this form of medusæ found about Jamaica seems to be a desideratum. I suppose, however, that for our purpose in this paper it will make little difference which name is used, the two forms being so similar in form and structure. I have, therefore, decided to retain both the names used by Conant.

For the complete anatomy of Charybdea the reader is referred to Dr. Conant's dissertation, "The Cubomedusæ" (8b), or the *Johns Hopkins University Circulars* (8a), both published by the Johns Hopkins Press. But, for the convenience of those who may be less familiar with Cubomedusan anatomy, the following brief summary of the anatomy of Charybdea is given:

The Cubomedusæ, as the name implies, approximate cubes, with their tentacles (four in Charybdea) arranged at the four corners of the lower face of the cube. These tentacles are said to lie in the

interradii. Half way between any two points of attachment of the pedalia (the basal portions of the tentacles) and a little above the margin of the bell (cube), in a niche, hang the sensory clubs, one on each side, four in all. Each sensory club hangs in a niche of the exumbrella and is attached by a small peduncle whose axial canal is in connection with one of the four stomach-pockets and in the club proper forms an ampulla-like enlargement.

Each club is said to lie in a perradius, and, like the tentacles, belongs to the subumbrella. This is shown by the course of the vascular lamellæ, bands of cells that, stretching through the jelly from the endoderm to the ectoderm all around the margin, form the line of division between sub- and exumbrella.

Each club has six eyes. Two of these on the middle line of the club facing inwards are called the proximal and distal complex eyes, to distinguish them from the four simple eyes that are disposed laterally, two on each side of the line of the two complex eyes. All of these eyes look inwards into the bell cavity through a thin transparent membrane of the subumbrella. Besides the eyes and the ampulla already mentioned, a concretion fills the lowermost part of the club, and a group of large cells, having a network-like structure and called network cells by Conant, fill the uppermost part of the club between the proximal complex eye and the attachment of the club to its peduncle (Plate II, Fig. 13). What is evidently nerve tissue, fibers and ganglion cells, fills the rest of the club, with two groups of large ganglion cells disposed laterally from the network cells. A sensory (flagellate) epithelium covers the club.

Most Cubomedusæ, among them Charybdea, have a velarium (comparable to the velum of the Hydromedusæ), a membrane of tissue that extends inwards at right angles all around the margin. This velarium, like a velum, has a central opening through which the water is expelled from the bell-cavity when the animal pulsates. In the perradii and in the angle between the velarium and the body wall, are the frenula, which give support to the velarium much like brackets support a shelf, except that here the brackets are above the shelf instead of below.

In the upper part of the bell is the stomach, with the phacelli in its interradii, and continued ventrally into the manubrium, or the proboscis. The cavity of the stomach is continued in the perradii through the four gastric ostia into the four stomach pockets, which

occupy the sides of the bell and extend to the margin. Immediately below the gastric ostia, and in the bell cavity, are the suspensoria, one in each perradius. These support the floor of the stomach much as the frenula support the velarium, except that the suspensoria are placed under the shelf (to continue Conant's figure) and not above it as are the frenula.

A nerve ring, underneath the epithelium of the subumbrella, passes from near the origin of each pedalium at the margin to the origin of the peduncles of the sensory clubs, a little above the margin, giving off a branch to each club. Eight ganglia are found in the course of this nerve. The four pedal ganglia lie near the bases of the pedalia, and are hence interradial; the four radial ganglia lie near the bases of the peduncles of the clubs, and are perradial. A small nerve, radial nerve, can be traced a short distance upwards from each radial ganglion. Underlying the epithelium of the frenula and the suspensoria are ganglion cells and nerve fibers in larger numbers than elsewhere (excepting the ganglia mentioned) in the subumbrella. Otherwise, ganglion cells and nerve fibers underlie the epithelium of the subumbrella, including the inner surface of the velarium, as also do muscle fibers, except in the perradii and in the region of the nerve, where the latter become interrupted.

PHYSIOLOGICAL.

Charybdea.

Light and Darkness—Experiments 1–9, 10, 33, 34.—As already stated in the Introduction, a part of Conant's experiments were performed in a photographer's dark-room, with the animals in a deep glass jar. In the dark a fair proportion of the animals became nearly quiescent on the bottom, but upon lighting a lamp many started up immediately, while others took a longer time to come to the surface and swim. These experiments were tried a number of times and on different occasions with very similar results. Some medusæ, however, tried immediately after being brought in, seemed not to react so well upon being placed in the dark-room, nor would they become quiescent. This, probably, was due to the fact that the animals had not yet recovered from the effects of being caught and placed in new surroundings. (Experiments 1, 2, 3.)

Other experiments (4–8, 33, 34) were tried by carrying the jar with the animals from the weaker light of a room into the more intense light of outdoors or into direct sunlight. The usual result was an inhibition of pulsation and a settling to the bottom, while the medusæ immediately became active again upon returning with them to the room. These results were so marked that no doubts can be entertained as to their cause, though some exceptions occurred in which animals placed in the sun continued to swim on the surface or soon recovered pulsation. In some experiments, too, no animals responded to the inhibitory stimulus of the brighter light or all very soon recovered. (See, however, Temperature.)

Reducing the light by placing a coat over the jar produced the same effect in some experiments (8, 9, 10) as did reducing the light in other ways, while removing the coat produced the same effect as exposure to brighter light. In these instances it appears to be the transition from weaker to stronger light that inhibits pulsation, rather than the actual intensity of the light; and *vice versa*. It must be noted, too, that when left for some time in any one place

the animals changed, some coming to the surface and others going to the bottom.

These experiments show beyond doubt that Charybdea is sensitive to light, and that it is moderate light that stimulates the animals to activity, while darkness and strong light inhibit activity. While the individual exceptions, as Conant himself suggests, are well explained on the supposition of individual diversity, yet it appears that other conditions, such as the time of day, temperature, etc., may have been responsible for some of the exceptional experiments in which no animals responded as expected.

While light of any intensity seems to have stimulated Romanes'[I] Sarsia and Tiaropsis (Hydromedusæ) to activity, we note that it is moderate light that stimulates Charybdea. This fact is evidently correlated with the circumstance that Charybdea usually lives upon or near the bottom.

It may further be added in regard to Romanes' Tiaropsis polydiademata, that when it was suddenly exposed to light it went into a spasm preceded by a long latent period during which there was a "summation of stimulating influence" in the ganglia. Sarsiæ would congregate toward the source of light and in general were more active in light than in the dark, while sudden darkness often inhibited a swimming bout. Romanes proves for Sarsia that the marginal bodies are the seat of luminous stimulation and that it is the light rays and not heat rays that stimulate. He also remarks that he has obtained similar results on the covered-eyed (Scyphomedusæ) medusæ, namely, that they respond to luminous stimulation.

It may here be of interest to note a few observations made by myself at Wood's Holl, Mass., on a beautiful Olindiad, which is abundant in the Eelpond at the above place. I found that in a room, in the ordinary light of evening, the animals swam actively; but the moment the electric light was turned on they stopped swimming and settled to the bottom or attached themselves to a branch of some weed or stem suspended in the water. This was the result in every trial. It is found, further, to be little active during the brighter parts of the day, when one must dip quite deep with a net in order to obtain it. A similar observation is also made by Murbach[II], who further states that this medusa may be deceived into laying its eggs by placing it in the dark.

One cannot help but remark how analogous is the behavior of medusæ, in respect to light and darkness, to the behavior of many of the higher animals,—and medusæ are among the most lowly organized of the animal creation.

Were one to conclude from the behavior of Charybdea in light and darkness in the laboratory, that it remained on or near the bottom in the daytime but became more active near or at the surface evenings, nights and early mornings, one would probably not be far from the truth. Dr. Conant, while towing near the bottom with a weighted net, in water four to five feet (1.2–1.5 m.) deep not far from shore and deeper farther out, found Charybdea in abundance mornings and afternoons, but very few in the evening. In the evening some few were usually taken in the surface tow. (See Introduction, Occurrence and Activity.)

Again, who knows but that Charybdea is active during the day, on the bottom where it was dredged (the light there would only be moderate), and quiet at night. This supposition would seem to be true, at least, for those forms of Cubomedusæ that live in deep water. We can hardly suppose that they should regularly rise to the surface from great depths and become active. This much we do know that bright light inhibits Charybdea's activities, while it probably would not be active in perfect darkness.

I do not know just what interpretation to put upon Conant's finding Charybdea at Port Henderson at the surface during the early part of the forenoon, before the sea-breeze roughened the water ("Cubomedusæ" p. 7). This fact hardly fits in with my conclusions above. Perhaps Charybdea's habits vary with its habitat.

Finally, while I find no experimental evidence in Conant's notes about what parts of Charybdea are sensitive to light, yet it would seem preposterous, from histological evidence and from Romanes' results on Sarsia, to doubt that the eyes of the marginal bodies are the seat of this stimulation.

Dr. Conant further experimented by cutting off certain organs and parts from the Cubomedusan bell. These excisions consisted chiefly in cutting out the concretions of the sensory clubs, cutting off the whole club, eliminating a part or whole of the margin and the velarium, cutting the bell into sectors, excising the stomach and parts connected with it, and other parts.

Concretions—Experiments 10, 11.—The four concretions were removed from each of four animals. Two of these (Experiments 10, and another (X), not appended, to save space) seemed to be little if at all affected by the operation. One of the two (10) swam actively, at first up and down more changeably than those intact, but later mostly near the surface. The other one also swam actively and showed nothing to indicate weakened sense-perception. The other two (11) did not stand the operation well, as Conant remarks, and immediately went to the bottom, where they remained, one swimming, while eight hours later one was still in good condition.

Several attempts with stronger light by removing the coat from the jar made no difference in the behavior of 10; it continued to swim as heretofore. Upon a final trial, however, with removing the coat, it went to the bottom, thus showing a possible reaction to light; but when next seen it was keeping to the bottom.

That the concretions should function as organs of light sensation, as the first of the above animals might seem to indicate, I believe is out of the question.* The fact, too, that this same animal (10), together with another (X), swam actively, immediately changing their course upon coming to the surface, in reality behaving quite as normal animals, hardly permits us to conclude from the behavior of the other two (11) that the concretions function directly as organs of equilibrium or space relations. May these concretions not function simply as weights for keeping the sensory clubs with their eyes properly suspended? Since these concretions lie at the lowermost part of the clubs and in closed sacs and unsupported by cilia, it would seem that the above suggestion as to their being weights is not improbable. Direct observation (Experiment 20) by Conant shows, furthermore, that the clubs always hang with a tendency for the concretions to be lowermost, regardless of the position of the animal.

Again, while they may function as weights, as just explained, the fact that the epithelium of the clubs is flagellated (a flagellum, continued as a nerve fiber, to each cell—see Histology), the supposition lies near that these flagella are the ones influenced by the concretions as the clubs bear against one side of the sensory niche or the other.

*It was at one time supposed that the concretions in the marginal bodies of medusæ represented lenses and the surrounding nerve tissue the optic nerve, a supposition so highly improbable that it never gained any acceptance. (Ib., p. 41, note.)

A somewhat similar view seems to be held by other observers and is noted by Lang in his text-book ("The outer epithelium of the auditory body carries the auditory hairs"). It seems, then, that in functioning as weights for suspending the clubs, they may also serve at the same time for making the pressure of the club against the niche greater than if they were absent, and thus in part serve in equilibrium. On this supposition we should expect, furthermore, that after the removal of the concretions the animal would be little, if at all, affected, since the clubs themselves, without the concretions, would still be of sufficient weight to be influenced by gravity and thus to bear against the walls of the sensory niche. It must be noted, however, that Conant's experiments upon equilibration in Charybdea are negative. Also, that Charybdea has any auditory sense is negatived by two attempts of Conant's with a violin—one attempt with the violin near the animals, and another with it in contact with the dish. (From an unpublished note.) Hence, some other word such as sensory or equilibrating should perhaps be substituted for "auditory" in the above quotation.

Removing the concretions from Aurelia gave negative results very similar to those on Charybdea. (Experiment 42.)

Sensory Clubs—Experiments 12–19, 20, 24.—The entire sensory clubs were removed from a number of animals. A paralysis of pulsation followed by a rapid recovery was the usual result. In some instances, however, there was no paralysis, while in others no recovery followed paralysis. This is true in a general way whether one club only or all were removed. While no permanent paralysis followed the removal of one or two clubs, yet permanent paralysis did occur after the removal of a third club, as, of course, also after the removal of a fourth. It is evident, too, that as the removal of the clubs progressed recovery seemed to be weaker after each cutting, except in one case when pulsation seemed to be quickened after the removal of a second club. The pulsations after recovery seemed to be not so strong and regular, often quite feeble, and in one instance in groups. Pieces of tissue with a club attached and pulsating regularly, ceased pulsating after removal of the club, in one instance, however, still giving occasional contractions.

These results are quite the same as those of Romanes[I] on Aurelia, Cyanæa, etc., and of Eimer[IV] on Aurelia, Rhizostoma,

Cotylorhyza, etc.* In these forms Romanes sometimes obtained complete paralysis after the removal of the sensory clubs only, as also after the removal of the whole margin, though this was not marked in Aurelia. In Cyanæa and other forms motor centers seemed to be more abundant than in Aurelia, so that paralysis was oftener followed by recovery. He concludes that while the principal motor centers reside in the lithocysts, other centers doubtless exist that may function vicariously, but that the centers of the margin are more definitely limited to the marginal bodies in the Scyphomedusæ than in the Hydromedusæ, in which the whole margin seems to be replete with centers. He feels positive, furthermore, that no motor centers exist in Aurelia's margin outside of the marginal bodies (lithocysts). Eimer's results are essentially the same as Romanes', so that for a more detailed comparison of the two, Romanes' works should be consulted.

Romanes' conclusion for the Hydromedusæ is that the motor centers are not so definitely localized in the marginal bodies, but in the margin generally, the excision of the marginal bodies alone producing only partial paralysis, as would also the removal of the margin from between the marginal bodies, but not so marked. For the Hydromedusæ he concludes, then, that all the centers of spontaneity are definitely localized in the margin, but not limited to the marginal bodies. To this he mentions one exception, namely, *Staurophora laciniata*, in which another center is found near the margin and two others in two opposite arms of the proboscis.

I made the remark in an abstract (VI) on Conant's notes that Romanes did not obtain recovery of pulsation after removal of all the lithocysts in Aurelia. As noted above, he did obtain recovery, so that Conant's results on Charybdea and also Aurelia (see Polyclonia and Aurelia) are quite in agreement with Romanes.

The paralysis following the removal of the clubs in Charybdea is evidently, primarily, the result of a loss of a part of its nervous mechanism (motor centers), and, secondarily, of nervous shock, and points to the existence of a definite nervous mechanism in the clubs. The histological evidence is here, as usual, corroborative of the physiological.

Another interesting phenomenon observed after the removal of

* Eimer's results I get from Romanes and Hesse[III].

one or all of the clubs was the strange behavior of the proboscis. This would reach from side to side, expanding and contracting its lips as if trying to grasp something. This behavior is very similar to that of the proboscis of *Tiaropsis indicans* when Romanes stimulated any part of its subumbrella, or of *Limnocodium sorbii*, a little fresh-water medusa, when he stimulated its margin or the region of the radial canals. (Ib., p. 242.)

I may add that I observed a very similar movement of the proboscis of the Olindiad, before mentioned. When I pulled off pieces of its gonads by means of quick jerks, with a small forceps, it would continually reach toward the injured part of its subumbrella. This medusa is generally quite active with its proboscis and can occasionally be seen to reach with it.

Romanes states in one place that the proboscis is not affected by the excision of the margin. This is evidently not the case in Charybdea, in which excision of the sensory clubs (which really belong to the margin—see "Cubomedusæ") decidedly stimulated the proboscis to active movements. This, furthermore, points to the marginal bodies as being organs of considerable importance in giving information in the life of Charybdea. In Romanes' Sarsia and other medusæ, however, the proboscis did respond to the stimulation of the tentacles and the marginal bodies, as also would the bell respond to a stimulation of the proboscis (manubrium), thus showing a reflex nervous connection between these regions of the bell, similar to that described for Charybdea.

Velarium and Frenula—Experiments 18, 29, 30, 41c.—"The power of originating contractions" to use Conant's own words, "evidently resides in the velarium or in ganglion cells of the frenula, just as it does in the proboscis and the floor of the stomach." Isolated pieces of the velarium contracted by themselves as did the whole velarium when all other tissue had been removed. An isolated velarium with the margin and the pedalia attached gave irregular contractions. When the pedalia with the *interradial ganglia* were removed it still contracted; and when all the other tissue was cut off contractions continued.

Cutting the velarium caused the *pedalia* to be strongly contracted inwards so that the tentacles were brought inside the bell. Cutting away the velarium did not interfere with the pulsations of the bell, but progress was much retarded.

Cutting the frenula caused the pedalia to contract but seemed not to affect the ability to swim. Comparing the velarium of the Cubomedusæ with the velum of the Hydromedusæ, I recall no observations similar to the ones here noted, though it seems that the two may have quite similar functions. It seems somewhat probable that the velum, and also the velarium, may function in obtaining food,—and this besides their function in swimming. Their probable function in swimming, as is well known, is evidently to narrow the mouth of the bell and thus to cause the water to be forced out in a smaller but more rapid stream, giving the animal a steady and more prolonged movement through the water at every contraction of the bell. In regard to taking food, I observed that a small crustacean, in the process of being swallowed by an Olindiad, seemed to be held by the velum being firmly contracted about it while the proboscis was working itself over the crustacean. It would seem, furthermore, that my supposition is supported for Charybdea by the fact that the pedalia and tentacles were contracted so as to be brought inside the bell when the velarium was cut. The stimulus of cutting the velarium may be comparable to a stimulus from some object touching it, and thus cause the pedalia and tentacles to come reflexly to aid in capturing or holding the object, a fish, crustacean, or such, to be captured.

Pedalia, Interradial Ganglia, Tentacles—Experiments 15, 23, 27–31, 41b.—When the pedalia were removed, the power of the animal to guide itself was completely gone. When one pedalium was cut the others contracted, while stroking the outer edge of the pedalia, touching the sensory clubs, or sharply pricking the subumbrella, often produced the same result. (See also Nerve.) The upper part of the subumbrella seemed not so sensitive and more seldom produced the reflex of the pedalia, while the base of the stomach did not give it at all. Stroking the outer edge of the pedalia of *Tripedalia cystophora*, the second of the two species of Cubomedusæ described by Conant, also caused the pedalia to be contracted inwards. I may note here that the muscle fibers under the ectoderm of the pedalia are specially well developed at and near the inner and outer edges, both in Charybdea and Tripedalia. On the flattened sides of the pedalia the muscle fibers are fewer.

When the pedalia were cut off far enough up to remove the interradial ganglia, coördination was not affected and the animal

could pulsate well enough but with little progress. (See above under Velarium and Frenula.)

An isolated tentacle is capable of squirming contractions, and when stimulated at either end, it would contract wholly or in part only.

The pedalia, then, it would seem, serve also as a steering apparatus, for which they are admirably fitted, considering their blade-like thinness.

Considering, now, the reflexes noted under this head and the preceding one, we find that there is an intimate nervous connection between the velarium and frenula, subumbrella, sensory clubs, nerve, and a single pedalium, on the one hand, and the pedalia on the other hand. This is born out fully, furthermore, by the histological evidence —(See Introduction and "Cubomedusæ"). Considering the subumbral plexus of ganglion cells and fibers, including the velarium and the frenula, which is in connection with the nerve ring and this again with the sensory clubs and the interradial ganglia at the bases of the pedalia, we have a basis for these reflexes. While Conant failed to demonstrate nerves ("Cubomedusæ") from the interradial ganglia to the pedalia, yet, that a nervous connection exists between the pedalia and the bell is well shown by his physiological experiments. I have, furthermore, demonstrated ganglion cells under the ectoderm of the tentacles (see Histology).

Romanes obtained quite similar results in the Hydromedusæ. He found that when a tentacle of Sarsia was slightly stimulated, it alone would contract, but when it was more strongly stimulated the other tentacles also would respond as also the manubrium. I find no evidence in Conant's notes of any such response of the manubrium of Charybdea, except when the clubs were cut off.

The reflex obtained on stimulating the subumbrella of Charybdea, when the pedalia would contract, is somewhat different from that obtained by Romanes, who found that the most sensitive part of the subumbrella in producing a reflex of the margin was at the junction of the manubrium to the bell and that the subumbrella below this point did not give the reflex.

Stomach, Suspensoria, Proboscis, Subumbrella—Experiments 12, 18, 19, 24–26, 29, 31.—The proboscis and the stomach with the phacelli when cut out, contracted with or without the lips removed. The isolated lips also contracted (twitched).

Pieces of the sides connected only with the stomach and suspensoria, or with the margin (Experiment 47 (?)) twitched spontaneously, but seldom did so when these were removed. In one instance the whole side was cut out so as to exclude the radial ganglion but still connected with a portion of the suspensorium. This pulsated, or contracted, but on being halved transversely, the lower half ceased to contract while the upper half connected with the suspensorium, continued to contract.

Cutting off the whole stomach end of the animal excited to very rapid pulsations of the remaining part, with the stream of water stronger out the aboral end than past the velarium.

Conant says, "It seems I get no good evidence of the subumbrella without connection with special nerve centers being able to contract by itself." The piece in which he did get contractions he suspects may have been intimately associated with some part of the frenula or the suspensoria. In Polyclonia no such doubt exists, for small pieces of subumbrella were seen to contract. A small piece of subumbrella of Charybdea with a sensory club attached could contract by itself.

From the above it would seem that a center capable of inciting to contractions resided in the suspensoria as well as in the sensory clubs, and this may be one of the centers that becomes potent upon the removal of the clubs. This is further supported by Conant's observation (Introduction and "Cubomedusæ") that an extra large number of ganglion cells is found under the epithelium of the suspensoria. A somewhat similarly located center of spontaneity described by Romanes for *Stauophora laciniata* (Hydromedusa) has already been noted.

As to the rapid pulsations of the bell after cutting out the stomach end, this also is similar to Romanes' results on Aurelia and other Scyphomedusæ, when he cut off parts of the manubrium or an aboral ring out of the bell. In these instances, however, Romanes soon obtained a slackening of the rhythm following the temporary acceleration. The temporary acceleration he attributes to the stimulus of cutting, and the slackening to a lack of some afferent stimulus from the removed tissue. Conant obtained the same results on Polyclonia by removing the oral arms (see Polyclonia) but says nothing about a slackening of the rhythm in Charybdea. I believe the increased rhythm in Charybdea was in part due to the decreased

amount of labor necessary to force the water out of two openings instead of one, namely, past the velarium. Just how much this observation bears upon Romanes' theory of rhythmic contraction, that the rhythm is due to an alternate exhaustion and recovery of the contractile tissue, as opposed to the ganglionic theory of rhythm of physiologists, one does not wish to speculate much. Yet, I feel that the observation rather supports this theory. The tissue having to do less work, would become less exhausted at each contraction and require less time for recovery and hence have a more rapid rhythm.

I here sum up Romanes' theory in a few words. The ganglia liberate a constant and comparatively weak stimulus, one perhaps about minimal. This stimulus sets off the contractile tissue; but as the tissue contracts and becomes exhausted the constant stimulus becomes, in relation to it, sub-minimal, and it does not contract again until it has recovered and the stimulus is again strong enough to set it off. The ganglionic theory of rhythmic contraction supposes that the ganglia liberate stimuli to the contractile tissue at successive intervals. Romanes had this theory suggested to him by the rhythmic contractions he succeeded in obtaining by subjecting deganglionated bells to a continuous but weak faradic stimulus, or by placing them into weakly acidulated water, or into 5 per cent. glycerine. Romanes claims that his theory better explains muscular tonus and the contraction of involuntary muscle. He does not, however, hold this theory to the exclusion of the ganglionic theory, since only too often does he speak in terms of the latter. He further brings in his support the fact that the frog's tongue, in which no ganglia have been demonstrated, can be made to contract rhythmically when subjected to a weak and continuous stimulus. He also calls attention to the rhythmic contractions seen in the Protozoa, the snail's heart, etc. Finally, physiologists are much inclined to explain the rhythmic contraction of the heart and other involuntary muscles, in part, at least, as due to a property of the contractile tissue.

Margin, Radial Ganglia, Nerve—Experiments 18, 21–23, 30.—Complete removal of the margin did not stop pulsation; but the removal of the radial ganglia stopped it permanently. While this experiment seems to have been tried only once, yet, taking into consideration the results of other operations, it would seem that the principal centers of spontaneity reside in these ganglia. (It should

here be remembered that the interradial ganglia were probably removed at the removing of the margin.)

Cutting the nerve in the eight adradii caused the *pedalia* to bend inwards at right angles to their normal position but did not in the least affect the coördination of the sides. When, however, the sides were cut in the eight adradii to the base of the stomach, coördination for the main part ceased, and each side pulsated in its own rhythm.

I have said that the principal centers of spontaneity reside in the radial ganglia. Upon further thought this hardly seems warranted. No doubt, among the principal motor centers must be placed the ganglionic masses of the clubs, and the radial ganglia, together with the homologous interradial ganglia, represent centers of equal value. I speak of these two sets of ganglia as homologous, since strictly speaking, they both belong to the margin, and the clubs at whose bases they lie probably represent modified tentacles. Conant's experiments leave us in the dark as to the function of these ganglia. Next in order, it would seem, are the ganglion cells in the suspensoria, as is suggested by the contractions of an isolated side with a portion of a suspensorium attached. (See previous head.) While we have seen that the frenula and the velarium can contract by themselves, yet, I find no evidence that these can impart their contractions to any adjacent tissue.

Conant's results on cutting the nerve eight times and then continuing the cuts to the base of the stomach are quite the same as Romanes and Eimer obtained upon Aurelia. Romanes, however, concludes that in his Sarsia, Tiaropsis, etc., coördination was broken when only short incisions were made in the margin. Charybdea appears, then, to agree with Aurelia rather than with the Hydromedusæ. Yet, since Romanes at first obtained similar results to those of Charybdea on Sarsia, but on further experimenting concluded that coördination had really been destroyed at the first cutting, we cannot speak with certainty that coördination had not been destroyed in Charybdea before the cuts had been continued to the base of the stomach. I say not with certainty, because the injury to the bell being slight, coördination may have been maintained on the principle of a simultaneously (simultaneous for the octants) alternate exhaustion and recovery of the contractile tissue on the principle of Romanes' theory.

Stimulation.—Romanes found when he stimulated a deganglionated bell of a Hydromedusa, that it responded by a single contraction, while that of a Scyphomedusa responded with several quite rhythmic contractions. Charybdea in this respect agrees with the Scyphomedusæ. Romanes' results were also verified on Aurelia. (Experiments 12c, 15, 50, 51.)

Activity of Charybdea.—In speaking of the activity of Charybdea, I cannot do better than refer the reader to the notes. (Experiment 41.) Conant remarks in his dissertation what an active swimmer Charybdea is, and this is further borne out by his later observations.

Temperature.—Ice in the water seemed to have no effect, except when held against an animal, when a slowing of pulsation followed in a few instances. On some pulsating actively in the sun the temperature of the water was found to be 92° F. (Experiments 33–35.)

Conant does not tell us how cold the water became when he placed ice in it, but judging from his results, it seems that he might have obtained a decided slowing of pulsation if the water in which the medusæ swam had been permitted to approach anywhere near the freezing point, say 35–40° F. Romanes obtained decided slowing of pulsation, and even complete inhibition, on a bell of Aurelia, as also a lengthening of the latent period on some strips cut from a bell of Aurelia, by lowering the temperature of the water. Replacing Aurelia in warmer water had the effect of immediate recovery and increased rhythm. In Aurelia, raising the temperature increased the rhythm but diminished it when the temperature of the water became 70–80° F. After a slowing of pulsation due to such a rise of temperature, it would not quicken again when the animal was placed in water of its normal temperature. Romanes explains this by supposing that the tissue of the medusa had been permanently injured by the abnormally high temperature. It would be interesting to observe how the tropical Aurelia behaved under such treatment, seeing that Charybdea pulsated actively and without apparent injury in water at 92° F. *Limnocodium*, noted by Romanes, and probably a tropical species, lived happily in water at 85° F. in the lily house of the Royal Botanical Society. The temperature of the water could be raised to 100° F. before it proved fatal to this medusa. Such facts point to a decided difference in the constitution of the protoplasm of tropical and

temperate medusæ. Romanes' Sarsia became frantic when placed in milk-warm water.

While writing the above, I was led to wonder whether the temperature of the water may not have been the stimulating influence in those experiments on light (previously noted) in which the medusæ continued to swim actively in the sunlight.

Food and Feeding.—See Experiment 36.

I again make note of a few observations made by myself on the Olindiad. A crustacean became entangled in the tentacles of a medusa; apparently this wished to retain it, for the proboscis reached in the direction of the crustacean, which, however, got away. I then placed, by means of a needle, another small crustacean against one of the tentacles. This was seized but not retained, for the animal pulsated and it was washed away by the water. Twice I saw a good-sized crustacean in the proboscis. In one instance the velum appeared to hold the part of the crustacean not yet in the proboscis. I noticed another with a crustacean wholly in the proboscis, which was much lengthened out, the upper part of the crustacean being in the stomach. The next morning the crustacean was wholly in the stomach and the proboscis normal. At 5.30 P. M. the crustacean was ejected, nothing but the shell and some rubbish remaining.

These medusæ seem to pay no attention to being touched by one of their kind, except to give a pulsation or two.

The proboscis appears very "intelligent" in its actions.* First, some of the tentacles can be seen to contract and to bend inwards, then the side next the tentacles contracts and the proboscis is seen to reach in that direction. I could not see, however, what the irritant was.

Occurrence of Charybdea—Experiments 37–40.—Dr. Conant's remarks ("Cubomedusæ") on the occurrence of Charybdea at the surface of quite shallow water and near the shore (which is quite at variance with former observations, that the Cubomedusæ are essentially deep-sea forms) are further borne out by his observations at Port Antonio. As already noted in the Introduction, Charybdea was here found in abundance in quite shallow water and near shore, but on the

* By no means do I wish to attribute intelligence to these animals.

bottom instead of at the surface as at Port Henderson. It is possible that the animals had been active near the surface earlier in the morning and that some unknown conditions determined their settling to the bottom earlier in the former place than in the latter.

Conant's conjecture, "whether these were their natural conditions, or whether the two forms," Charybdea and Tripedalia, "were driven by some chance from the deep ocean into the harbor and there found their surroundings secondarily congenial, so to speak," seems to be borne out in favor of the former supposition (for Charybdea at least),—that these are their natural conditions and that Charybdea Xaymacana is essentially a shore form.

Aurelia and Polyclonia (Cassiopœa)

Experiments 42–53.

Many of the observations on these forms relate to the rate of pulsation. In an Aurelia, following the removal of a lithocyst, there was a pause followed by pulsations. In about two minutes rhythmic pulsations were renewed. Four minutes after the operation there were nineteen pulsations to the half minute, while twenty minutes after there were only nine, and these in groups of six and three. The normal rate of pulsation was twenty-five to the half minute.

Polyclonia behaved much in the same manner as Aurelia. Upon the removal of lithocyst pulsations continued, but in groups with short pauses. The normal rate of pulsation was twenty-seven to the half minute, while three minutes after the operation it was seventeen, and eleven minutes after, fifteen to the half minute. The tissue connected with a removed lithocyst gave contractions. Placing a Polyclonia in fresh sea-water more than doubled the rate of pulsation, which, however, soon fell to the normal rate, and lower in one instance. In small individuals the rhythm is decidedly more rapid than in those of larger size. The few observations on this point would seem to show that it is in inverse proportion to the squares of the diameters of the bells.

The removal of a single oral arm or of the whole eight, in Polyclonia, had much the same effect as the removal of a lithocyst: there was a decided slowing of the rate of pulsation, while the immediate effect of cutting was an acceleration or a return to near the normal rate. About a day later this same animal had quite

regained its normal rate of pulsation and continued to live over two weeks. A long latent period followed the cutting of an arm, before the stimulation of cutting manifested itself.

An Aurelia, with all its lithocysts removed, still gave spontaneous and coördinated contractions after allowing time for recovery from the operation. This was the result in one instance, while in several others only a few contractions were observed. Removal of the sixteen marginal bodies (lithocysts) in a Cassiopœa produced paralysis for a time but recovery soon followed. A Polyclonia with its entire margin removed was paralyzed but had so far recovered in a day as to be able, at intervals, to give spontaneous pulsations.

The removed margin of a Polyclonia pulsated vigorously. This margin was then split so as to make a ring within a ring but connected at one point by a small bridge of tissue. The waves of contraction, which always originated on the ring with the lithocysts, passed the bridge to the inner ring quite as Romanes experienced. The outer ring was next split so as to separate the exumbral portion from the subumbral, when it was found that the contractions always originated from the latter. Seven days after its removal, this same margin was still alive and pulsating vigorously, and broken-off pieces of the subumbral portion were pulsating by themselves. Fifteen of the ganglia were removed. It was then found that while most of the pulsations originated at the remaining ganglion, now and then contractions originated in other parts where no ganglion remained. Two days later this margin was still alive with contractions originating as often from other parts as from the ganglion. A similar observation was made on a margin of Cassiopœa.

A Polyclonia with the eight lithocysts of one side removed, to compare with a normal one, gave no evidence of affected coördination.

An oral lobe from an Aurelia could give contractions some minutes after removal.

In another Aurelia a circular cut was made about the base of the oral lobes through the epithelium of the subumbrella. The animal could pulsate well enough but coördination seemed a little affected, while in another one with a like cut but semicircular, no effect was noticed.

These results on the removal of the lithocysts (and margin in Polyclonia) in Aurelia, Polyclonia and Cassiopœa agree quite with those on Charybdea and, of course, also with Romanes' and Eimer's

results as to paralysis and recovery following the removal of the lithocysts, or margin, in Aurelia, Cyanea, etc. I recall no similar observations, however, on removing a single lithocyst, and the question of an explanation for the slowing of the rhythm thus brought about arises. Romanes gives as an explanation for the slowing of the rhythm (Aurelia, Cyanea, etc.) following the temporary acceleration upon removing the manubrium or a portion from the center of the bell, as due to a lack of an afferent stimulating influence upon the ganglia from the excised tissue. May a similar explanation not serve to explain the slowing following the removal of a single lithocyst, above noted? The removed lithocyst could no longer give its efferent stimulus to the remaining ganglia nor to the tissue, so that the former would have a weaker stimulating influence, in consequence of which the latter (the contractile tissue) would be deprived of a part of the original stimulus of the remaining ganglia as also of that of the removed ganglion. The whole would thus result in giving to the contractile tissue a weaker stimulus, which, again, would require longer and greater recovery on the part of the tissue in order to be set off by the stimulus at hand. This explanation is given on the basis of Romanes' theory of rhythmic contraction previously explained.

Of course, it may be suggested that the musculature had lost tonus, due to the lack of influence of the removed ganglion (lithocyst), in consequence of which there was a lowering of irritability on the part of the contractile tissue. This would require a greater summation of stimulating influence (Ganglionic theory of contraction) on the part of the remaining ganglia to set it off. Again, the loss of irritability on the part of the contractile tissue may have been due to a lack of nutritive influence from the removed ganglion.

Romanes' explanation, that the slowing of the rhythm following the removal of the manubrium and central parts of the bell in Aurelia and Cyanea is due to a lack of an afferent stimulus on the ganglia from the removed tissue, likewise explains the similar results obtained by Conant by removing the oral arms from Polyclonia.

The fact that a margin of Cassiopœa and also of Polyclonia, connected with but one ganglion, often originated contractions in other parts as well as from the ganglion, seems to show that motor centers resided in the margin outside of the ganglia. This would be somewhat at variance with Romanes' conclusion, that no

such centers existed in the Scyphomedusæ. Conant does not state whether the Polyclonia margin in question was kept in fresh sea-water or whether the water was not changed during the seven days. If the latter is the case, then some poisonous compounds may have been formed that acted as a stimulus much as weakly acidulated water served Romanes in producing rhythmic contractions in deganglionated bells.

Again, while it is true that no ganglia are known to exist in the margins of the Scyphomedusæ outside of the ganglia in the marginal bodies, yet, ganglion cells and nerve fibers are found in the sub-umbral part of the margin as well as in the rest of the umbrella. And as I know no reason why scattered ganglion cells may not function as ganglia, it is possible that the contractions in question were spontaneous.

Finally, is it possible that the remaining ganglion originated the contractions in different parts of the margin, thus acting at a distance from the points at which contractions originated? Romanes gives an instance in which he believed to have evidence that this was the case. Upon a final consideration I am inclined to this latter explanation.

Summary.

Summing up for Charybdea, we have seen that it is very sensitive to light, strong light as also darkness inhibiting pulsations, while moderate light stimulates it to activity. Also, a sudden change from weaker to stronger light, or *vice versa*, may inhibit or stimulate to activity respectively. This behavior of Charybdea seems to be correlated with its habit of life on the bottom. We have no reason to doubt but that the eyes of the sensory clubs are the seat of light sensation.

The experiments on equilibration are negative, giving us no certain light on the function of the concretions, though it appears that they may serve, in part at least, for keeping the sensory clubs properly suspended. Their function in giving the animal sensations of space relations is not, however, excluded.

Excision of the sensory clubs demonstrates that they are the seat of important ganglionic centers, the removal of which results in temporary paralysis and weakness. That they also are the seat of organs (eyes, network-cells, concretions) that are of importance in

giving information in the life of Charybdea, is evident from the reaching motions of the proboscis after the removal of the sensory clubs. Other centers of spontaneity in their order of importance probably are: the radial ganglia (one experiment); the interradial ganglia (?); the suspensoria, as shown by their supplying stimuli to isolated pieces of the sides connected with them; the frenula and the velarium, the latter of which gave contractions when removed with the frenula or in pieces only. No evidence is given that the frenula or the velarium can impart their contractions to other tissue, though this seems probable for the former. The proboscis can also contract of itself.

Reflexes between the velarium, frenula, subumbrella, sensory clubs, nerve, and any one pedalium, on the one hand, and the pedalia on the other hand, are very common, and point to the pedalia with the tentacles as organs of defense and offense. The pedalia serve also as rudders in swimming.

Finally, as judged by the results in this paper, Charybdea seems to occupy, physiologically, a position intermediate between the Hydromedusæ and the Scyphomedusæ. In its great activity as a swimmer, in its response to light, and in its reflexes it is Hydromedusan, while in the paralysis and recovery following the removal of its marginal bodies, as also in its response with several pulsations instead of one, when a deganglionated bell is stimulated, it is Scyphomedusan.

The observations on the Discomedusæ, Aurelia, Polyclonia, Cassiopœa, demonstrate the existence of motor nerve centers in the marginal bodies; but that other centers are present is shown by the recovery of pulsation following the removal of the marginal bodies or the margin. These results are mainly confirmatory of those of Romanes and Eimer. They differ from these in the fact that margins of Polyclonia and Cassiopœa, with only one ganglion attached, originated contractions distant from the ganglion. Removing of a single lithocyst resulted in a slowing of pulsation, as did also the removal of the oral lobes, though the immediate effect in the latter case was an acceleration. Isolated pieces of the subumbrella could contract.

DR. CONANT'S NOTES.

Below follow Dr. Conant's notes. They are printed about as Conant left them. Their order of succession, however, has been

changed to bring similar experiments together, while useless and often repeated ones have been omitted, and short elliptical sentences completed. Where the present writer wished to add any explanation, the same has been placed in brackets.

Charybdea.

Light and Darkness.—1. Eight medusæ, in a deep glass jar and covered by a black coat, except one inch around the top, were placed in the dark-room.

a. When light from a lamp was thrown on the surface (one inch) layer, the animals were active near the surface; when the light was withdrawn, one or two were on the bottom and not moving but were probably pulsating.

b. After four or five minutes in the dark, three or four besides a feeble one are on the bottom. It took about two minutes to get them all to swim [by the lamp]. Of the three on the bottom, one, at any rate, was not pulsating. [Three other attempts like a and b were made, with very similar results.]

2. Experiment No. 1 was repeated several weeks later. Four in a large round glass dish were placed in the dark-room. A lamp being held to the dish all but one were found to be on the bottom. That one quickly went to the bottom, while two of those on the bottom quickly came to the top. In two or three minutes the one that had gone to the bottom began to pulsate and at about the same time the other one that had remained on the bottom also began to pulsate, while the two that had gone to the top stayed there swimming very actively. [Repeated with like results.]

3. Fresh ones did not show the reaction to light after darkness so well as did those in the experiments previously recorded. They were experimented with about nine A. M., while usually they were tried later in the day. I had rather suspected from previous work that they would not react so well when fresh.

4. a. In walking with the jar (1) of jelly-fish of experiment 1 from the dark-room to the back porch of the laboratory (fifty steps), in the bright sun and a cool breeze, all were found upon entering the laboratory door to have settled to the bottom and most of them to have ceased active swimming. In five minutes two or three were swimming somewhat, and in five minutes more all but one or two (eight in all) were swimming.

Walking with the jar about the laboratory did not suffice to make any change in their swimming, nor did blowing on the surface make any appreciable change.

b. Upon taking the jar to the back porch and placing it on the stone or cement flags, in the shade and a cool breeze, in four minutes time all were on the bottom not even pulsating.

Upon replacing them on the laboratory table all began to swim about at once. [Repeated.]

c. The jar (1) was placed on the back porch again; in fifteen seconds three were on the bottom; in one-half minute all but one. In three or four minutes all were on the bottom, but two were swimming lively and the others pulsating. In another minute all were swimming.

d. The jar (1) was tried again, not resting it on the flags but holding it by my hands on the sides. The effect was just as quick; they stopped pulsating at once. By the time I had got back to my table in the laboratory, one was at the surface and another arrived just as the jar was set down.

[Several other experiments of an order similar to those just noted were tried, with very similar results.]

5. Two buckets stood side by side in the laboratory. One bucket (1) had more Charybdeas in it than the other bucket (2), and also had more since brought in (about an hour). The water of one (1) was also more discolored and with more organic matter (sea weed, etc.). In the laboratory the animals were active on the surface of both buckets. Placed in the sunlight on the porch, no breeze, the sun slanting so that one side of the water in the buckets was bright while the other side was shaded, the jelly-fish in (1) went mostly to the bottom, while those in (2) seemed unaffected though some showed a tendency to go to the bottom after a longer exposure. The experiment with (1) was repeated and it took some five minutes for them all to go to the bottom. In a few minutes after replacing them in the laboratory several were active again on the surface.

6. Jar (a) with five large ones stood on my table; they were quite active. Placed in the sun (no breeze), on the porch, one or two sank to the bottom at once and the others seemed to slow their activities somewhat but not very markedly. In a few minutes all were swimming, apparently more actively than before, in the bright sunlight.

[In other experiments Conant shows that it is not the stimulus of walking that causes them to swim when carried into the room, for they would not swim when he walked with them on the porch. Also, he shows how they may change, some swimming, others not, when left for some time in any one place.]

7. In a tumbler were two pulsating very vigorously. Placed in the bright sunlight, very little breeze now and then, they showed no change whatever.

8. Some in a jar were covered with a black coat. The coat was taken off, and almost immediately they stopped pulsating, or pulsated but feebly, and sank to the bottom. The coat was put on again with one part near the bottom of the jar exposed. Almost at once, the animals, which were quite motionless, pulsating but little, resumed pulsation, which became more and more vigorous, and quickly swam to the top again. It seems plainly to be a reaction to light. [Such experiments as this were repeated at different times with very like results.]

9. A bucket with several bobbing actively on the surface was set out in a smart shower, and the animals continued bobbing on the surface as before. I could not see that they made the slightest attempt to go below.

There can be no doubt but that there is an individual difference in sensitiveness to the reaction of light after darkness. E. g., I just removed the coat from a dish with four in it; one went to the bottom at once, another presently, a third remained active at the surface, the fourth when noticed was on the bottom.

There is also a difference in the length of time they stay on the bottom as well as in the quickness in the response to light. Some recover very quickly, should say in less than a minute, and at once become very active. Some stay for a long time and only resume activity upon the coat being placed over them. Perhaps this explains some of the observations in Experiment 1.

Sensory Clubs.—10. All four concretions were removed and the animal stood the operation well. It swam more restlessly, however, than others did in the same surroundings. It seemed at first to show a trace of loss of sense-perception. It swam up, and down again, more changeable than those intact, which stay rather more constantly either on the bottom or at the surface. This may, however, have been

due solely to the restlessness of the animal after the operation. Later it swam actively for by far the most part on the surface only, which points to the truth of the preceding statement.

It showed no reaction to *light*. A coat placed over the jar was removed, when it was found to be on the surface and it remained there. This was twice repeated. I noticed specially that on pushing the bell above the surface of the water it at once turned and went deeper as the normal animal does. Finally, given another trial with removing the coat from the jar, it went to the bottom as the normal animal usually does. After this, when next seen, it was keeping to the bottom. [This experiment was repeated on another occasion with almost identical results, no loss of sense-perception being noticeable.]

Sometimes it seemed as if access of *light* at removing the coat acted as a stimulus to one or more of those that were quiescent on the bottom. This was noticed again on the following day.

11. Two more were operated upon. These did not stand the operation well and stayed on the bottom, one swimming, while eight hours later one was in better condition (pulsating) than two left in the same dish for comparison.

12. a. Three clubs were cut off leaving only the stalks. A temporary paralysis of the power to swim was the immediate effect. Later it partially recovered this power. The proboscis, which was previously quiet, now showed convulsive twitchings and movements. It continued for some time to move to one side and then the other (after short pauses of varied length) as if to grasp some object. The lips of the *proboscis* were also moving and at times expanding. Often the movements were towards the side on which the club was uninjured.

b. The fourth club was next removed. A temporary paralysis as before resulted, followed by a quick recovery of pulsation; but the animal was now much weakened. The movement of the proboscis continued—shortening, lips expanding, moving to this side or that. The pulsations of the bell were kept up even when too weak to swim.

c. The sensory niches of this same animal were treated with 2.5 per cent. acetic acid by means of a pipette. The stalks of all four clubs showed white. Pulsations ceased. The velarium showed feeble local contractions. The movements of the proboscis and suspensoria drawing down the stomach continued. Upon stirring the animal it

gave rather feeble, somewhat convulsive pulsations with local (fibrillar) contractions; the pulsations in some cases were pretty well coördinated, but were more on the twitching kind.

13. Three clubs were removed. The animal pulsated well, only a little less strongly, perhaps. After a minute or two the fourth club was removed. It pulsated almost immediately, perhaps thirty seconds after the operation. It swam very well and pulsated feebly five hours after the operation.

14. One from jar (a) (Experiment 6) was operated upon. When the first club was cut off there was a paralysis of pulsation followed by a quick recovery. Cutting off the second club seemed to stimulate pulsation, the third to diminish it; after cutting off the fourth club it still pulsated. When placed in a large jar it pulsated on the bottom, but not strong enough to swim. The pulsations were fairly regular and sometimes seemed to occur in groups of two, but these groups were not well marked.

15. Another one from jar (a) was taken. One club was cut out, upon which there was a very temporary paralysis followed by good pulsations afterwards. The *proboscis*, as in all cases noticed, gave active movements to this side and that side. These movements of the proboscis were often very quick and definitely directed as if a well defined stimulus were given. After the operation one *pedalium* contracted so as to be at a right angle to the main axis of the bell; shortly a second pedalium also contracted. Placed in a small round dish the animal swam actively.

A second club was removed, and it swam as well as before. After fifteen minutes it was not swimming but pulsating against the jar. Upon stirring it a little it swam vigorously ten to fifteen strokes and then stopped. It seemed weak and its movements appeared not so definite, though this might be due to weakness.

A third club was removed. The only change seemed to be rather greater weakness.

After about five minutes the fourth club was removed. Paralysis of pulsation followed. It had the power to contract its *pedalia* when these were rather vigorously stimulated with a needle. It also gave one feeble pulsation when so stimulated.

16. The sensory clubs were removed from another. After removal of the third one it still pulsated actively, but stopped completely and apparently for good after the removal of the fourth club. Another

one stopped pulsating apparently for good upon removing the third club.

17. All four sensory clubs were removed from one, cutting as high up as possible so as to remove the endodermal tract of nerve fibers of the peduncle. It pulsated afterwards apparently the same as if the stalks had been left intact.

18. A small piece surrounding a sensory club and including the *margin* can contract by itself. The piece observed pulsated with quick pulsations and rhythmically but intermittently. After a fresh cutting away of such a piece, the portion of the *velarium* attached was seen to contract rhythmically, while the rest of the *subumbrella* was not so seen. The part of the subumbrella above the radial ganglion that was cut off did not contract by itself. The same portion of the velarium cut off did give contractions.

19. A sensory club with the surrounding region cut out pulsated rhythmically; when the club was cut from the end of its stalk pulsation stopped. This observation was repeated on another, and contractions were seen after the removal of the club. A piece of the *subumbrella* wall from the same animal gave contractions now and then even after an hour.

20. The normal position of a sensory club seems to be with the concretion almost at the lowermost end; often with it certainly lowermost, but probably oftener with the perpendicular passing through the center of the attachment of the club to its peduncle and just by the inner edge of the concretion. The eyes point inwards.

When the animal is on its side the concretions are always quite lowermost. When the animal was inverted the tendency was for the concretions to be lowermost. In this position the eyes may point in several directions. In one instance those of one club pointed rather outwards, while of two other clubs they pointed more in the plane of the body wall. (See also Experiments 24, 29.)

Nerve.—21. Cutting the nerve eight times, once on each side of each sensory club, produced no loss of coördination in pulsating. The animal was weakened, however, by the operation, which was made drastic to insure cutting the nerve; but it was still able to swim. This experiment was repeated four times.

22. That coördination was continued after the nerve was cut was proved beyond doubt by cutting from the edge up (eight times)

so as to perfectly separate the sensory clubs and the pedalia. Pulsations continued synchronously in all four sides—not the slightest evidence that one side contracted out of time with the others.

23. The eight cuts were made as in the preceding experiment with no loss of coördination noted. When the cuts were carried up to the base of the stomach, however, coördination ceased. The four side pieces seemed to contract each in its own time. Only two sides could be observed at one time, and they at any rate did not contract synchronously. One side often gave two contractions while the other side rested or gave one.

Yet, a little later, three of the sides at any rate showed a pretty good coördination. The fourth was smaller and did not seem to get into the game much—it went more on its own schedule. The four pieces were then cut apart and placed together under a dissecting microscope. No coördination at all could be made out. No evidence, therefore, of any definite rate of pulsation inherent in the sensory clubs.

Cutting the nerve causes the *pedalia* to forcibly contract inwards.

Side, Subumbrella.—24. A whole side was cut out, the transverse cut being above the sensory organ so as to take off [leave off] the radial ganglion also. This pulsated, or rather contracted, nicely. The upper end had been cut just through the *suspensorium.* It especially gave twitchings like the twitchings of the stomach. The piece was then halved transversely, when the upper part containing the portion of the suspensorium twitched as before while the lower part was not seen to contract again. This was repeated with the same result, except that a portion of the lower part gave a slight contraction several times. The part that contracted was at the upper end of the piece, *i. e.*, nearest the *suspensorium.* The contractions were also more longitudinal than transverse, as the regular contractions would be.

The piece connected with the sensory clubs of course pulsated nicely. Upon cutting off the sensory club from the stalk, pulsation ceased, but twitching of the *velarium* continued. This was repeated with the same effect.

In the same animal, in cutting off the sides, the stomach was left, the cut being through the gastric ostium. The floor of the *stomach* was now cut off by cutting out the four interradial points of

attachment. The stomach and the proboscis gave vigorous contractions and tied themselves all up so that I could not cut off the proboscis.

The four pieces of the floor of the stomach left on the interradii gave contractions nicely. The phacelli continued their squirming movements.

25. Cutting off the whole aboral end of the animal excites to very rapid pulsations of the remaining part. The stream, as shown by particles in the water, is apparently stronger out the aboral end than past the velarium.

It seems that I get no good evidence that the subumbrella is able to contract of itself without connection with special nerve centers. In the one case noted (Experiment 31) I could not be sure but that the part that contracted was intimately associated with the suspensorium or frenulum.

26. A piece of the subumbrella cut off and having, so far as I could determine, no connection with ganglia, frenula, or suspensoria, gave contractions. Another piece was not seen to contract.

A small piece of the subumbrella connected with a club can contract. The proboscis can give contractions of itself when cut off with the base of the stomach. Even a cut-off lip can twitch by itself. A portion of the subumbrella by itself also showed twitchings. (See also Experiments 18, 19, 25, 26, 29, 47, 49.)

Pedalia, Velarium, Radial and Interradial Ganglia.—27. The pedalia with their tentacles were cut off at their bases to insure cutting out the interradial ganglia. The animal could pulsate well enough, but intermittently and without much progress (the velarium, of course, being injured). Cutting one pedalium caused the others to contract.

28. When the pedalia were cut off from one, the power of direct motion was entirely gone. It swam in circles, turned summersaults, changed its course continually, the oral end getting ahead of the aboral end, or trying to do so. The whole power of balancing was gone. It seemed excited by the operation and swam continually. [Repeated.]

29. The pedalia can be made to contract inwards by stroking their outer edge with a needle. This was noted last year and has been seen several times this year. Their inner edge is not so sensitive.

Touching a *sensory club* caused the pedalia to contract inwards in two cases.

The pedalia could be made to contract by giving the subumbrella a prick,—generally a rather severe one was necessary. The upper part of the subumbrella seems not so sensitive as the lower part and the proboscis, and the base of the stomach did not give any reflex at all (two specimens). One of the two could be made to give the reflex only with much difficulty. This was a very lively one. It would even stand severe pricks on the nerve, or even through the region of the sensory clubs, without contracting the pedalia or stopping pulsations.

Cutting the frenula seemed not to affect the ability to swim well. Cutting in this region brings about the reflex of the pedalia.

In the preceding fish the *velarium* was cut away wholly in some places, in other places it was left only as ragged strips. The pedalia became very strongly contracted and the *tentacles* were brought inside the bell. Pulsations that seemed strong produced much less progress than with the velarium intact. [Repeated.]

30. One with the whole *margin* cut off still gave pulsations. Upon the removal of the region of the *radial ganglia*, however, pulsations were seen no more.

The *velarium* in the above continued to give twitchings. The four pedalia were cut off with plenty of the tissue at their bases to insure the removal of *interradial ganglia*, and twitchings of the velarium with irregular contractions continued. No full contraction all around the velarium was noticed. When all the tissue was trimmed off as nearly as possible down to the *velarium*, the latter still gave twitchings and irregular contractions as before,—even more so as if excited by the operation. The power of originating contractions evidently resides in the velarium or in the ganglion cells of the frenula just as it does in the proboscis and the floor of the stomach.

Small pieces cut from between the pedalium corners and the frenula, so as to have tissue on them from neither, could contract by themselves. (See also for Pedalia, Experiments 15, 23, 41b; Velarium 18, 41c.)

Tentacles.—31. A cut-off tentacle can contract by itself, sometimes with squirming contractions. A prick at either end can produce a forcible contraction. A slight prick at the distal end may produce a local contraction. The proximal end is more sensitive, but this difference is not very marked. One with only the tentacles removed seemed to be a little less able to guide itself well.

Proboscis, Stomach, Phacelli.—32. The lips of the proboscis are highly contractile by themselves. The movement of the stomach and the phacelli goes on, after the lips are cut off, with increased vigor, due to the stimulus of shock. The vigor and frequency of their contractions, however, diminish quicker than that of the cut-off lips. (See for Proboscis, 12, 15, 18, 26, 29; Stomach, 18, 24, 29, 31; Phacelli, 18, 24, 31.)

Temperature.—33. Temperature does not seem to have much effect. Some placed in a tumbler half full of water, in the bright sunlight, swam vigorously over three-fourths of an hour. The water was quite warm to the hand.

34. The above experiment was repeated with the same results. A thermometer placed in the water with them showed 92° F.; hung in the sun near by, it showed 94° F.

Ice in the water did not stop their pulsating temporarily or permanently, except that it did for a short time after being held against one. Even then it took some time (fifteen to twenty pulsations) before it produced any effect.

35. Ice placed in the water again showed no marked effect. They swam as lively as ever. Some, after pulsating against the ice for a little while, seemed to be less vigorous, but quickly recovered in another part of the jar. Others did not seem to be the least bit affected by contact with the ice.

Food and Feeding.—36. I tried to feed one. A red and a white copepod were put into the subumbrella cavity. No attempt to eat it was observed in either case, though the copepods remained in the subumbrella cavity for some time.

Animals found in the stomach of Charybdea: small fish were most frequently seen; at another time a small stomatopod; again, a small polychæte; small shrimps; amphipod.

Those taken on August 16th (3 to 4 P. M.) seemed to have, for the most part, food in the stomach, and this more so than those taken in the morning.

Occurrence of Charybdea.—37. In the first tow on the bottom (with a net made of mosquito-netting and weighted with rocks in order to sink it) the haul was forty. I do not think that we could have been towing more than four or five minutes. The time was

about seven A. M. A light breeze was blowing and there had been a heavy shower a half-hour previous.

38. The usual time of towing was about 6.30 to 7.30 A. M. The water was four to five feet (1.2 to 1.5 m.) nearest shore but deeper farther out. At this time of day one could count on getting plenty of the larger sized (15 to 20 mm.), many small ones, but very few of the smallest. This was the experience of several mornings.

On August 12th I towed about nine A. M., and got but few of the larger sized, many small, ones, and very many of the smallest.

The next day (7.00 to 7.45 A. M.) those obtained were mostly of the larger size. On the same day (3 P. M.) others of the party towed at the same place and obtained but few.

On another day I towed in the afternoon (3 to 4 P. M.) and obtained great numbers as I usually did in the morning.

39. We towed about 7.30 to 8.30 at night. Very few Charybdeæ were taken. On this evening we towed five times in the same locality, and obtained but seven or eight specimens. Towing with the same net on our way home, it was filled with Aureliæ and five or six Charybdeæ. It seems as if Charybdea came to the surface at night. Those towed in the evening were dead the next morning.

The next morning Richard, our colored attendant, towed from 5.30 to 6.30. There were heavy showers. The usual find of large and medium ones was obtained. There were only two with planulae.

40. The material of September 2nd was obtained about six A. M. They were mostly of large size. In all only fifteen or twenty were taken. Richard explained the small number by saying that the bottom had changed in the locality where we usually towed and that he got no weeds in his net, but mud.

The next day more were brought in by Richard (6.30 A. M.) There were rather more than yesterday but the quality was the same. There were three with planulae.

On another morning Richard brought in a great many, about a hundred. Among these there were three with planulae (light-colored and budding); on a previous day there was one with the reddish-brown kind and with a mouth.

Activity of Charybdea.—41. a. About five o'clock in the morning a Charybdea was taken in the tow. It was in good condition swimming incessantly round and round without change of direction,

in a jar of about twenty centimeters in diameter. It came to the surface every now and then, after eight to fifteen pulsations. The tentacles and the phacelli were of a lilac shade. If a pencil was placed in its way it would pulsate against it repeatedly without any effort to dodge around it.

6.58	A. M.,	124	pulsations	were	counted	to	the minute.
8.00	"	124	"	"	"	"	"
9.25	"	136	"	"	"	"	"
10.15	"	131	"	"	"	"	"
11.00	"	146	"	"	"	"	"

At 10.15 it went around the dish in eight seconds, taking eighteen or nineteen pulsations. If a bright platinum spatula or a black pencil was placed in its circuit it would repeatedly butt against it each time it came around. After the second or third pulsation against it, however, it seemed to have some sense to change its direction.

b. The *pedalia* have no perceptible action of their own. They move inwards slightly toward the axis at each pulsation, but scarcely as much as one would suppose from their attachment to the pulsating margin. It seems as if they were for "winging" the moving animal more than for anything else.

c. The *velarium* is loose and it flaps. It seems to take part in swimming something more than the passive diaphragm function,—i. e., it straightens out during the recovery after each contraction of the bell.

Aurelia and Polyclonia.

[The following experiments were performed at Port Henderson, Jamaica, in 1896.]

42. May 12th. An *Aurelia* was pulsating normally at the rate of twenty-five or twenty-six pulsations to the half-minute. One lithocyst was cut out, when a few contractions, evidently caused by the stimulus of cutting, followed; then, rest. In the first minute there were only about five pulsations. In two or three minutes rhythmic pulsations were resumed. Four minutes after the cutting there were nineteen pulsations to the half-minute. About twenty minutes after there were nine to the half-minute, in groups of six and three.

A *Polyclonia*, about four and one-half inches (115 mm.) in diameter, gave twenty-six or twenty-seven regular pulsations to the half-minute. After one otocyst was removed, pulsations continued, but in groups with intervals of pause: *e. g.*, thirteen, pause; ten, pause; six. Three minutes after the removal of the lithocyst there were 5, 3, 1, 3, 5, or seventeen pulsations to the half-minute. Eleven minutes after the operation there were fifteen to the half-minute. The removed lithocyst and surrounding tissue gave contractions.

43. May 13th. The *Aurelia* was in rather poor condition but would pulsate upon being stirred. The other seven lithocysts were removed when only a few contractions originated thereafter.

The *Polyclonia* was in good condition, but was pulsating only intermittently when first seen in the morning. When the remaining seven lithocysts were cut out and no more pulsations were observed, the oral arms could still move.

May 14th. Both were found dead upon returning in the evening.

44. May 15th. An Aurelia and a Polyclonia were taken in the morning. The *Aurelia* was two and one-half to three inches (62.5-75 mm.) in diameter, with three tufts of phacelli, three oral arms and seven lithocysts. The *Polyclonia* was normal and seven or eight inches (175–200 mm.) in diameter.

In the *Aurelia* all the lithocysts were removed. Spontaneous and coördinated contractions could still occur after time had been allowed for the shock from the operation to pass away. The next day the animal was still alive and pulsating, but ragged, and the next day following was quite dead.

In the *Polyclonia* the normal rhythm was fourteen pulsations to the minute. Some pulsations were apparently quicker than others and the intervals were not the same. Thirteen, ten, and twelve pulsations were also counted. After putting the animal into fresh sea-water, it pulsated thirty-three to the minute. Six minutes later it was still pulsating at the same rate, while in four minutes more eleven pulsations, many of which were in groups of two, were noted. In five minutes more it pulsated eleven times to the minute with only one double pulsation. One *oral arm* was then cut off and the rhythm counted about one minute afterward—fourteen pulsations, then a pause of fifteen seconds, then two pulsations, in all sixteen to the minute were counted. About ten minutes later there were eight pulsations, two or three minutes later only three, while in two or three

minutes more only three. There was a long latent period—two or three seconds—before the stimulation of cutting off the arm made itself evident in the rhythm.

A second oral lobe was removed. Then there followed twenty-four pulsations, a pause of two seconds, and two pulsations, in all twenty-six pulsations to a minute. The rate of pulsation soon fell to the previously abnormal low rate.

Third lobe removed: 21 pulsations in first half minute and then 16, or 37 per minute.

Fourth lobe removed: 17 pulsations in first half-minute plus 13 gives 30 for the minute.

No difference in the coördination of the animal was shown as a result of the removal of one-half the number of oral arms.

Fifth lobe removed: 17 pulsations plus 15 equals 32 to the minute.

Sixth lobe removed: 17 in first half-minute plus 4 in the second half-minute gives 21 pulsations for the minute.

Seventh lobe removed: 17 plus 9, or 26 per minute.

In all these instances the rhythm in the second half of the first minute was irregular and intermittent.

Seventeen and then seven pulsations were provoked after the animal had become quiescent, or nearly so, by merely handling it.

45. Eighth oral lobe was removed and pulsations stopped. The next day the animal was in good condition. The pulsations counted in the evening were 12, 14, 14, 11, per minute. The rhythm was not regular; there was a tendency to groups of twos, threes, or more, but no prolonged intervals of rest were observed. When placed into fresh sea-water, the pulsations were fourteen to the half-minute or twenty-six to the minute; seventeen to the half-minute, and thirty-three to the minute were also counted. This specimen gave spontaneous contractions during two weeks, after which it was thrown out, the aboral end being eaten through and little or no regeneration having taken place.

46. Two more were operated upon: A. Its rhythm was 18, 14, 17. Its entire margin was cut off. The separate pieces of the margin pulsated, 6, 7, 4, 6, 7, 9. The animal seemed paralyzed by the operation; it responded by a contraction now and then to stimulation but gave no spontaneous pulsations. B. Its rhythm was 17, 15, 12, 12. All its *oral arms* were removed. Its rhythm was only raised to seventeen and not perfect. In twenty-five minutes it had fallen to eleven, in four hours to ten pulsations [per minute].

May 22nd. A and B are living as also the pieces of the *margin* of A; all are giving spontaneous pulsations now and then at comparatively long intervals—even A, with its margin removed.

May 26th. Everything is still living. The one with the margin cut (A) counted sixteen and nineteen pulsations per minute, though this was not kept up all the time.

June 2nd. A and B and pieces are still living and contracting spontaneously. It is now two weeks, and they were thrown out eaten through at the aboral end with little or no regeneration.

47. The margin was cut off another one (C) and it was then paralyzed. The margin contracted vigorously by itself. The margin was next split, but a connection of about one-half an inch wide was left between the two rings. Over this bridge the contractions passed from the outer and inner ring. The inner ring did not originate any contractions. Both rings were then cut near their connecting bridge of tissue and the larger ring with the marginal bodies was split longitudinally so as to separate the exumbral from the subumbral portion. It was found that the contractions started only from the subumbral portion while the exumbral portion did not contract at all.

June 5th. Five of the eight small pieces of C were not seen to contract either to-day or yesterday. A slow rotary motion was observed in some of the pieces suggesting ciliation, but no cilia or currents pointing to ciliation were seen with a low power. C was seen to pulsate spontaneously. Possibly it did yesterday but it was not watched closely. A piece of the subumbral surface of C broken off (not from the margin) was found to contract spontaneously.

48. June 6th. In a fresh one (D) from Port Royal, the eight lithocysts of one side were removed in order to compare its movements with an intact one. Coördination was apparently unaffected.

June 9th. The margin of C is still pulsating vigorously. Parts of the subumbrella broken loose from the strip pulsated by themselves now and then. Fifteen lithocysts were removed, leaving only one at the end of the strip. It was found that with this single ganglion (lithocyst) left, and originating most of the contractions, now and then a contraction would originate at another part of the strip where there was no ganglion. Three days later contractions originated as often from other parts as from the ganglion.

Cassiopeia.

[The remaining experiments were all performed in 1897, at Port Antonio.]

49. Removal of the sixteen marginal bodies caused paralysis for a time; then recovery followed.

Contraction was limited to the subumbrella.

A portion of the *subumbrella* not from the margin can contract by itself as well as a portion of the margin with the marginal bodies (lithocysts).

In the *margin* cut off as a strip with only one marginal body attached at one end, contractions sometimes started from the opposite end.

Aurelia.

50. Size, seventeen or eighteen millimeters. Pulsations, thirty-two. Lithocysts, nine. The operation consisted in the removal of the concretions with as little injury to the pigmented parts of the marginal bodies as possible. One whole marginal body, however, was removed in the operation. Soon after the operation the pulsations were 28, 26, 20, 20, per minute.

Another one; size fifteen millimeters. Pulsations were forty per minute. The operation consisted in the removal of the concretions and pigmented parts of the marginal bodies with as little injury to the adjoining parts as possible. After the operation it seemed as if the intervals between the pulsations were irregular,—not a series at regular intervals. An hour or so after the operation the pulsations were very intermittent. During the afternoon it was not seen to pulsate except when it was stirred up, when six or seven vigorous pulsations followed. These, however, were rather aimless.

51. One sensory club (marginal body) was cut out, including its basal part also. In one or two other cases more or less injury was done to adjoining parts also. Pulsations ceased upon the removal of the last club, but upon placing it in an aquarium and allowing it to come to rest for two or three minutes, pulsations were now and then seen. In the evening, this one and another did not pulsate except when stirred, when they pulsated with good progress.

52. A circular cut, about two inches in diameter, was made through the epithelium of the subumbrella around the base of the

oral lobes. The animal pulsated well enough, but the contractions seemed not so simultaneous in all parts of the margin as normally. After a few days it had partly regenerated but died. One of the oral lobes cut off had some power of contraction, and this some time after the operation. A similar cut, but semicircular, made no difference between the contractions of the two halves.

53. The whole region of the sensory clubs was cut out when the animal was not seen to pulsate again, except in the evening, when pulsations were observed. The oral lobes also moved.

HISTOLOGICAL.

Method.—The following results on the histology of the sensory clubs, their eyes, and the tentacles, as already noted, were obtained from some of Dr. Conant's preserved material. These results relate almost wholly to Charybdea, with only a few references to Tripedalia, noted in their proper place.

A portion of this material was killed after keeping the animals in the dark for some time, for the purpose of discovering any changes in the pigment of the eyes. I believe that a retraction of the pigment of the long pigment cells that project between the prisms and pyramids of the vitreous body in the retina of the distal complex eye is very evident in eyes killed in the dark. (But more on this below.)

I obtained my best results from the material preserved in saturated corrosive sublimate, to which had been added (5 to 10 per cent.) acetic acid. This also was Conant's experience in his previous work on Charybdea and Tripedalia.

My best sections were obtained by embedding the sensory clubs in celoidin, passing the little blocks of celoidin with the sensory clubs into chloroform until perfectly transparent, and then into paraffine. I then cut sections as we ordinarily cut paraffine sections, mounted and stained them on the slide. My purpose in using this method was to avoid the displacement of the vitreous bodies of the eyes during embedding and cutting. This object was fully realized and more besides. Since the sections cut by the celoidin-paraffine method gave me so decidedly the best differentiation of the axial fibers of the retinal cells, as also of the cilia, basal bodies, etc., I am inclined to believe that the celoidin was in part responsible for this differentiation.

Most of my series were cut 4 μ in thickness. All in all I cut sixty-five clubs besides making some maceration preparations from material preserved for that purpose. These sixty-five series represent material from fourteen bottles. As a whole, my material was good, but the material from one bottle was decidedly superior for showing the axial fibers of the prisms and pyramids of the retinal cells. This shows the advantage of plenty of material. It will be evident that I had plenty of material.

I found iron-hæmatoxylin the most satisfactory stain. I stained for a shorter or a longer time—one-half to several hours and longer—and then washed out the sections until under a low power of magnification they appeared quite unstained, the nuclei and a few other parts only appearing darkly stained.

Depigmentation I practiced but little. I obtained many of my series almost wholly unpigmented, especially those I cut last. Others, of course, were very heavily pigmented. I am not certain but that alcohol slowly dissolves out the pigment after a long period of preservation. Slight variations in the technique of killing and preserving may also, perhaps, determine the stability or solubility of the pigment, as, of course, also the condition of the pigment at the time of killing.

Anatomy.—For a short epitome of the anatomy of a Cubomedusa and of a Cubomedusan sensory club see p. 2 of the Introduction.

The Distal Complex Eye—General.—The distal (larger) complex eye (Fig. 7) and the proximal (smaller) complex eye (Fig. 13) are so named to distinguish them from the lateral simple eyes of the clubs. The distal complex eye consists of the following parts: a cellular cornea, continuous with the epithelium of the sensory club; a cellular lens (externally cellular and internally often quite homogeneous) immediately beneath the cornea; a homogeneous capsule just internal from the lens, and evidently a secretion from the lens cells; a vitreous body composed primarily of prisms and pyramids just beneath the capsule; and a retina of pigmented cells, with subretinal nerve tissue, ganglion cells and fibers. To my knowledge all observers (except Carrière, who missed the capsule) are quite agreed on the anatomical structure of the distal complex eye as also

on the proximal complex eye and the lateral simple eyes.* It is on the histological structure of some of the various parts that differences exist.

Cornea.—Little need be said on the cornea except that it consists of flattened cells applied to the outer surface of the lens. It is continuous with the epithelium of the club and evidently a modified portion of this epithelium (Fig. 7). All observers conform to this statement.

The Lens.—The lens is of cellular origin, but in its interior the cells are often so changed—absence of nuclei, cell walls, and protoplasmic structure—as to make a mass quite homogeneous and structureless. While this internal mass sometimes shows practically no structure, yet at other times it is found broken up into masses much the size and shape of cells but without nuclei, while again, cells with nuclei may be quite evident. This occasional breaking up of this mass is evidently predetermined by its original cell structure. Iron-hæmatoxylin stains this inner mass very dark and it is difficult to wash out the stain. Borax carmine and Lyons blue give the best results on the lenses. In figure 7 the lens of the distal complex eye is shown as quite homogeneous internally, while in figure 13 (proximal complex eye) it is drawn cellular. In this latter lens the inner cells are quite round and nucleated as they may also appear in the distal eye. What I have said applies equally to the lenses of both complex eyes, though the cellular nature of the inside of the lens is more readily demonstrated in the proximal eye.

It appears that it is in younger specimens that the central mass of the lens shows the cellular structure best, and that as the animal grows older this structure is more and more lost until no trace

* Haake[2] says that in the adult *Charybdea Rostonii* the vitreous bodies of the complex eyes are absent but present in the young. It is difficult to explain this observation except on grounds of imperfect preservation of the adult material, for in all observations on other forms a vitreous body is described. Haake evidently did not use sections, and for this reason his results must be regarded as of doubtful accuracy. Haake also says that the simple lateral eyes of the clubs are absent in the adult, but present in the young.

of it remains. As concerns most of my series I could not well determine which were from younger and which from older individuals, yet, several series of quite small (5 mm.) and therefore young animals, in which the eyes were so small that the lenses were compassed into less than half a dozen sections, the cellular structure of the lens was very evident.

The external cells of the lens form a spherical shell (both complex eyes) which, in section, shows as a hollow ring (Figs. 7, 13). The thicker ends of these cells lie at the inner (toward the capsule) half of the sphere and the cells taper toward the corneal surface, dovetailing laterally with their immediate neighbors as also distally with those from the opposite side of the sphere. The thicker inner ends of the cells contain the large nuclei with nucleoli. At a point (*Figs. 7 and 13) on the inner (next the capsule) surface of the lens the cells only approximate each other and thus leave a place which is easily broken through, as is shown by portions (drops, probably representing cells or portions of cells) of the mass within the lens becoming squeezed out into the substance of the capsule and the vitreous body, and found occasionally also among the cells of the retina. A considerable portion of the inside of the lens may be found thus squeezed out, and its path can often be traced. This phenomenon is evidently brought about by a contraction of the shell of the lens during fixation and before the inside of the lens has become hardened.

In origin the lens is evidently ectodermal, originating from an ectodermal invagination which becomes pinched off as a hollow sphere, the outer (*i. e.* next the cornea) half of which becomes the lens, the inner half the retina (*i. e.* vitreous body plus the so called retina). (See Retina.) The transition from retinal to lens cells is quite readily made out at the lower side of Fig. 7, but the corresponding structure on the upper left side is not so manifest. It is further evident that the lens is again an invagination into this sphere, and the point at which the lens cells approximate (where the central mass of the lens may be squeezed out as above described) represents the place of pinching off of the original lens-retina sphere. It appears, then, that the lens is formed in the lens-retina sphere in the following manner: The cells of the secondary invagination going to form the lens begin to lengthen distally (*i. e.* toward the cornea) during their invagination to form a hollow sphere, at the

same time dovetailing with each other and budding off cells to form the inside of the lens (Figs. 7, 13).

At the lower side of the lens, near the margin of the retina, the cells of the lens are slightly indented or pushed inwards (Fig. 7, ind.). I believe this to be due to the weight of the lens in the normal position of the club, when the lens rests against the margin of the retina and the capsule and adjacent tissue.

Anticipating the description of the retina, it may here be added, that the retina is formed from the inner half of the lens-retina sphere. The cells of this portion of the sphere become differentiated into prism cells, pyramid cells, and long pigment cells, while laterally, beyond the margin of the vitreous body, they are differentiated into pigmented iris cells (Figs. 7, 6a).

Above are my results on the lens. Haake[2] speaks of the lens as consisting of a cellular "Kern" with a covering of lamellated cells. Carrière describes it as cellular and filled internally with a "Gerinsel," or coagulation. Carrière and Haake are each in part right. Claus describes it as wholly cellular. Schewiakoff regards the lens as wholly cellular, and like Claus has not noted that internally this cell structure may be quite obliterated. Schewiakoff regards the lens and retina as formed from an invaginated sphere, and shows the transition from the lens cells into retinal cells as I have figured. Conant also gives the structure of the lens for the complex eyes as cellular but missed the change of structure that the interior of the lens may undergo.

The Capsule.—The capsule of the lens (Figs. 4, 7) lies immediately below (inward from) the lens. In structure it is homogeneous, except for certain fibers from the long pigment cells of the retina that traverse it, while sometimes also other fibers can be seen which, possibly, are branches from the fibers just mentioned or continuations from the fine fibers of the prism cells of the retina soon to be described. I have, however, no evidence that the fibers from the prism cells extend beyond the prisms in whose axis they lie. The capsule lies very closely applied to the lens, never becoming separated from it in sections, and is, hence, regarded as a secretion from the lens cells. Just what its function may be is difficult to surmise. The proximal complex eye possesses no capsule. I have thought, however, that if the lens should be adjustable, the capsule might

serve as a protection to the prisms of the vitreous portion of the retina during the adjusting movements of the lens. (But more on this below.) To my knowledge all previous observers are quite agreed on the structure of the capsule. Carrière and Haake, however, missed it altogether.

Retina.—While I have enumerated (following previous observers) the vitreous body and the so-called retina as distinct parts, yet, as the sequel will show, they are, histologically, different parts of the same thing—namely the sensorium proper of the eye—and I propose to use the term retina for both taken together, while I retain the expression vitreous body (as hitherto used) for the vitreous portion of the retina. This simplifies matters; and using a word that is already used for analogous structures of other eyes (vertebrates, anthropods, molluscs) is conducive to clearness. I have been tempted, furthermore, to use the words *rods* and *cones* for the prisms and pyramids that I find in the vitreous bodies of the retinas of the complex eyes. But since the prisms in reality approximate prisms and the pyramids pyramids, in their shape, I have decided to retain the words prism and pyramid for these structures. The former of these terms (prism) was first used by Conant in his description of the complex eyes.

What I shall call the retina, then, in the distal and proximal complex eyes of Charybdea, consists of three kinds of elements: the prism cells, the pyramid cells, and the long pigment cells. (Figs. 4, 7, 22, prc, pyrc, lp.) We may also describe the retina as composed of three zones: the vitreous zone (vitreous body of authors), the pigmented zone, and the nuclear zone. (Figs. 4, 7, 22, vb, pz, nz.)

The cells composing the retina form a single layer in the shape of a hollow cup, into which cup the lens with its capsule fits. (Fig. 7.) This single layer of cells takes in the thickness of the vitreous zone, the pigmented zone, and the nuclear zone. Indeed, the distinctions vitreous zone (vitreous body), pigmented zone, and nuclear zone characterize three topographical regions of the retinal cells.

That the retina is made up of three kinds of cells is most readily demonstrated in transverse sections through the vitreous body. Fig. 1 is such a section, taken quite near the pigmented zone (at about the level x, Fig. 4). Three different kinds of areas are readily made out in such a section. The more numerous areas

(pr) are transverse sections of the distal prisms of the prism cells, the less numerous and lighter areas (pyr) are transverse sections of the pyramids of the pyramid cells, and the large oval heavily pigmented areas (lp) are the transverse sections of the long pigment cells. The dots within the two first named areas represent fine fibers in the axes of the prism and pyramid cells, to be described below. The presence of three kinds of cells can again be readily seen in such Figs. as 4 and 7, in which the elements of the retina are cut parallel to their long axis. (Fig. 22.) Again, a transverse section through the most distal part of the pigmented zone of a slightly pigmented retina (Fig. 2) also shows us the presence of three kinds of elements. The larger and more heavily pigmented areas (lp) are the long pigment cells; the smaller, lighter areas (pyrc) with a central dot are the pyramid cells, and the more numerous dots, with no definite polygonal areas outlined about them (prc), belong to the prism cells. Thus, I believe, we have conclusive evidence of the existence of three kinds of cells in the retina of the distal complex eye.

(a) The prism cells are the more numerous, and, as the name implies, end distally in a vitreous polygonal prism (Figs. 4, 7, 22, pr). The prismatic structure of the vitreous body is also shown in Figs. 10 and 11, which are drawn from a macerated preparation of Conant's. (See the descriptions of these figures.)

In Figs. 4 and 7 the prism cells correspond to the cells with the darker nuclei (npr); in Fig. 2 they are represented by the dots without defined polygonal areas about them (prc), and in Fig. 1 by the most numerous areas (pr). These cells, then, consist of a centrad portion with nucleus, a pigmented portion with granules of a dark-brown pigment, distal from the nucleus, and a distal vitreous prism which extends to the capsule of the lens.

In the axis of each prism is a fine darkly-staining fibril extending the entire length of the prism. I found no good evidence that this fiber extends into the capsule. Centrad this fiber is continued through the pigmented part of its cell and approaches to or near the nucleus (Fig. 2, dots without defined polygonal areas; Fig. 7, part of retina left unpigmented). In some instances I could trace this fiber quite to the nucleus, while in others it ended before reaching the nucleus or a little to one side of it. I am inclined to believe, however, that it extends past the nucleus and is continued as a nerve

fiber. I believe this to be so because the fiber is evidently sensory, and *a priori* we should expect it to be so continued. Further, I find decided evidence in sections of the simple eyes to show that the fibers there extend past the nucleus into the subretinal tissue where I could not trace them farther. (Fig. 16.) Again, that the flagella of the epithelial cells of the club are also continued into the cells, in some instances could be traced past the nuclei (Figs. 12 and 26), and the fact, too, that the retinal cups of the eyes represent invaginated epithelium (the axial fibers of the prisms are hence cilia?)—all this leads me to believe that the axial fibers of the prism-cells extend centrad past the nuclei through their cells and are continued as nerve-fibers. (See below under pyramid-cells and under epithelium). Immediately upon entering the pigmented part of its cell the axial fiber of a prism-cell has a dumbbell-shaped enlargement which lies quite at the distal edge of the pigmented part of the cell (Fig. 7, unpigmented part of figure). This, of course, can be seen only in unpigmented retinas. This dumbbell-shaped body, (Basalkörperchen of Apathy), which name I give it, since it evidently is homologous to the basal bodies described by others for the cilia of epithelia, can be most beautifully seen as two minute spheres lying close together and in line with the nucleus. These two little spheres of the basal bodies put to the test the highest powers of the microscope; but, when, after a prolonged and careful study, one satisfies himself of their existence and exact shape, the very difficulty with which they are resolved adds a zest to be appreciated. The length of a basal body is about one-fifth to one-fourth that of the nuclei of the prism-cells.

The structure of the nuclei of the prism-cells is that of a dense network (Figs. 4, 7, npr) which stains dark with hæmatoxylin. A nucleolus can often be seen in these nuclei. In some few series, again, these nuclei did not show a network-like structure, but the chromatin was arranged in masses (Figs. 5, npr). These nuclei can usually be distinguished from those of the other cells of the retina by their denser, darker-staining network (Figs. 4, 7, npr), or as shown in Fig. 5 (npr). Their denser structure and staining capacity are a distinguishing characteristic of the nuclei of the prism-cells. I must add, however, that not in every series is this apparent.

That portion of a prism-cell that contains the nucleus rarely contains any pigment; and when pigment is present, I believe that

it has been dissolved in from the pigmented zone. The nucleus, again, lies a little centrad from the pigmented part of its cell, so that an unpigmented zone is seen in the retina between the pigmented zone and the row of nuclei (Figs. 4, 7, 22).

Centrad the prism-cells are continued as a single process (Figs. 6, b, c, d, and 8a, b, c, d). In some sections I thought I could trace these processes to the basement membrane, but I could not satisfy myself that such appearances were not due to artificial splitting in the tissue. Schewiakoff makes a similar remark about his supporting cells, which cells I believe are the same as my long pigment cells, but these do not extend to the supporting lamella.

At the margin of the retina the cells do not develop prisms but remain pigmented and form an iris (Fig. 7), which was so named by Claus and also described by Schewiakoff. These cells also assume a somewhat different shape (Fig. 6a). This cell (Fig. 6a) is seen from its broader side with which it is applied to the capsule or the lens. Schewiakoff figures similar cells. That the cells of the iris are prism cells without the prisms does not necessarily follow. They simply represent cells of the retinal cup that have become differentiated to serve as an iris.

As to the exact origin of the prisms, and pyramids (to be described below), it is difficult to say anything definite. If the so-called basal bodies of the axial fibers are really homologous with the basal bodies of flagella, then it would seem that they (the prisms and pyramids) are secretions comparable to cuticular secretions.

(b) The pyramid-cells, like the prism-cells, are differentiated into three regions: a distal vitreous pyramid, a pigmented part, and a centrad part with nucleus. The pyramids are seen in transverse section in Fig. 1 (pyr) and in longitudinal section in Figs. 4 and 7 (pyr).*

Each pyramid extends between the bases of the prism-cells about one-third to one-half the depth of the vitreous body (Figs. 4, 7, 12 (pyr). The pyramids are also a shade lighter than the prisms,

* In the series from which Fig. 3 is taken the pyramid-cells are not so readily demonstrated. Indeed, I missed them altogether at first in this and some other series and supposed that there were only two kinds of cells (19), but upon a careful re-examination I could demonstrate them to my satisfaction. They did not show, however, in the particular section of Fig. 3, so that they are not indicated in this figure.

which fact is characteristic. In the axis of each pyramid is a darkly-staining fiber quite like the one described for the prism-cells (Figs. 1, 4, 7, 22). That this fiber extends distally beyond the limits of the pyramids I could not determine, but I do not think that it does. Centrad this fiber extends into the pigmented portion of its cell quite to or near the nucleus as was described for the fibers of the prism-cells (Figs. 7, 22). Whether or not these fibers extend past the nucleus and become continued as nerve fibers, the same course of reasoning holds as was given for the fibers of the prism-cells. Each of these fibers possesses a basal body just on its entrance into the pigmented part of the cell (Fig. 7), but I could not determine that it was dumbbell-shape. In form it represents an enlargement of the fiber itself, which gradually tapers again to its normal size. The continuations of these fibers within the pigmented parts of the pyramid-cells, as also the basal bodies, could only be demonstrated in unpigmented series.

Patten[5] describes axial fibers extending centrad through the rods (vitreous portions) of retinal cells ("retinophora") into the region of the nucleus and past the nucleus (arthropods and molluscs). My retinal cells (prism and pyramid cells) evidently correspond to Patten's retinophora, but I find no evidence that one of my retinal cells represents more than a single cell, while Patten gives evidence that his retinophora are made up of two cells closely applied to each other as twin cells. If this were also true for the retinal cells that I have described, I believe my macerated preparations would have shown it. Schreiner[12b] and Hesse[13] also figure and describe axial fibers for the rods of the visual cells in polychætous annelids, and Schreiner[12a] also for molluscs. Neither of these observers finds the fibers to extend distally beyond the rods nor centrad toward the nucleus as Patten and myself show. Neither Schreiner nor Hesse figures these cells as twin cells as Patten does, so that to my knowing Patten stands alone in this respect. Andrews[14] describes and figures rods for the visual cells of polychæte annelids but no axial fibers. He was the first to describe these rods in annelids.

The pigmented zone of the pyramid cells, in heavily pigmented series, is filled throughout with dark-brown pigment granules, and is quite like that of the prism cells (Figs. 4, 7). In transverse sections, however, through the most distal part of the pigmented zone, of unpigmented series (Fig. 2), lighter areas with central dots could

occasionally be demonstrated, which areas are the pyramid cells. In Fig. 2, the more definite polygonal outline as well as the lighter shade of these areas was a distinguishing feature. The difference in shade was not wholly due to a difference in pigmentation but to a structural difference.

The nuclei of these cells are usually a little larger than those of the prism cells and are filled with a finer and less dense network (Figs. 4 and 7, npyr), in consequence of which they present a lighter appearance in sections when examined with a high power. It will be seen in the figures (4, 7) with what regularity these lighter nuclei lie opposite the pyramids. Some few exceptions occur. These are probably due to the fact that a nucleus or pyramid was not differentiated by the technique. If this opposition between the pyramids and the lighter nuclei were all, I believe it would be sufficient evidence for associating these lighter nuclei with the pyramid cells.*

(c) The *long pigment cells* are about as numerous as the pyramid cells. In these cells, as in the prism and pyramid cells, three regions can be distinguished: the region of the nucleus, a pigmented region (the distal half of which extends between elements of the vitreous body), and a distal rod-like portion, or fiber, which is continued between the prisms into the capsule of the lens (Figs. 4, 7, 9). The pigmented portion is about twice the length of that described for the other cells, and also often of greater diameter, so that in transverse sections (Figs. 1, 2, 3) these cell-areas are larger than those of the other cells. As nearly as I could determine, these cells are pigmented just like the other retinal cells described. In quite unpigmented series, however, they often contain more pigment than the other cells do

*I go into this at some length because the cell-walls in the series that showed the nuclei best differentiated as lighter and darker ones did not show well, and there might be some doubt that these lighter nuclei belonged to the pyramid cells. I could, however, in many instances, trace the axial fibers of the pyramids through the pigmented zone to these lighter nuclei (as already noted) which fact can leave no doubt but that some of these nuclei belong to the pyramid cells. (Similar nuclei, however, are found to belong to the long pigment cells, to be described below.) Centrad these pyramid cells are continued into a single process just as the prism cells were shown to be (Fig. 7). Figures 6, 8, 9, and 21 show samples of all the pigmented cells found in macerated preparations, and none of these (except Fig. 9, long pigment cells) show more than a single centrad process. Hence, I conclude that centrad both the pyramid cells and prism cells are continued as a single prolongation.

(Fig. 2). Distally, the pigmented part becomes narrowed to a strong pigmentless fiber (Figs. 3, 4, 7). This fiber stains quite dark with iron-hæmatoxylin and appears homogeneous. It passes between the prisms into the capsule, where it usually bends in a direction toward the margin of the capsule (Fig. 7) and passes diagonally across this to the lens. In sections, a space is often seen about these fibers in the vitreous body, which I regard as a shrinkage space (Figs. 3, 4), since it is not evident in all series (Fig. 1). In Fig. 7, I have assumed that these spaces are due to shrinkage and have not indicated them. Also, in this same figure I have assumed that the spiral appearance of the fibers (Fig. 4) is due to a shortening of the prisms during fixation, and have drawn them straight. At the lens these fibers seem to end. In a few instances they were seen to branch upon reaching the capsule (Fig. 4). In Fig. 9, also, which shows some of these cells from a macerated preparation by Conant, the rods show evidence of branching at their distal terminations. In the same preparation I thought I could see that a fiber became expanded into a membrane spreading over one of the lens-cells. I could not satisfy myself, however, that this was the actual condition of things. Judging from Fig. 9, one might conclude that all the fibers are branched distally; yet, if such were the case I should have seen more of it in sections, but branching as seen in Fig. 4 is the exception. Hence, if all these fibers do branch, I am inclined to believe that it must be among the bases of the lens-cells. Or, if the fibers do expand into membranes to cover the lens-cells (I could not explain purpose), the evidence in Fig. 9 may be nothing more than fragments of this membrane left attached to the ends of the fibers. As is seen in Fig. 7, most of these rods end opposite the cells of the lens, and not usually between two adjacent cells as Schewiakoff has described for Charybdea marsupialis. The nuclei of these cells are like the nuclei of the pyramid cells (Figs. 4, 5, 7, 9) and often have a nucleolus.* Centrad these cells are continued into a number of processes as is seen in Figs. 5, 7 and 9. How far the several centrad processes extend and where they end I cannot say; but, as seen in Fig. 5, they soon taper to a thin end which I suppose may be continuous with a nerve fiber. I believe Schewiakoff was mistaken when he stated that these cells extend to the basement membrane.

*I have been able to demonstrate nucleoli in all the different nuclei of the cells of the sensory clubs.

I have found no evidence in these cells of the existence of an axial fiber such as I have described for the prism and pyramid cells. I find no definite arrangement of the nuclei of the retina into definite layers, but the nuclei of the three kinds of cells lie quite mixed, sometimes one kind lying deeper than the other as can be seen in the figures. Again, they may lie quite at the same level. (This point will be referred to later.)

It is these long pigment cells that I believe retract their pigmented part from between the prisms and pyramids when the medusæ are placed in the dark, protruding with their pigment when placed in the light. Fig. 5 is a section from a slightly pigmented retina killed in the dark. The parts of the cells projecting beyond the pigmented zone, and which would lie between the prisms and pyramids (here not shown) of the vitreous body are seen to be narrower than in sections from retinas killed in the light (Figs. 1, 3, 4, 7) and the cells themselves appear in a condition of retraction as is shown by their large centrad portions with the nuclei, which latter, also, here lie at quite a lower level than the other nuclei. (The pyramid cells were not shown in this series.) I occasionally found appearances like Fig. 5 in retinas killed in the dark (indeed, in some the pigmented portions in the vitreous body were much thinner and more retracted than in Fig. 5). Yet this appearance was not of sufficiently general occurrence to leave no doubt as to its significance. As positive evidence, however, I cannot give it any other interpretation than the one given—that the cells retract themselves with their pigment when in the dark. Again, it must be added that the nuclei of these cells may occasionally lie quite deep even in retinas killed in the light. Indeed, like structures in different retinas may vary considerably in size and shape. None of my darkness retinas, however, showed such a large proportion of the pigmented parts of the long pigment cells projected between the prisms and pyramids as did the light retinas. I examined and tabulated all my series with respect to the extent the long pigment cells were projected into the vitreous body, and I found that those which showed these cells with their pigment least projected between the prisms and pyramids to be those that had been killed in the dark. I thus feel satisfied that the pigmented parts of these cells become in part or quite completely retracted from between the prisms and pyramids of the vitreous body when in the

dark, but just how this is accomplished—whether the whole cell with its nucleus takes up a deeper position, the cell substance at the same time collecting in the region about the nucleus, as shown in Fig. 5 and the diagram (Fig. 22), I cannot with certainty state. It would seem, too, as though the pigment became less in the cells exposed to darkness, for I rarely, even in the most retracted heavily pigmented series, saw the pigment to extend farther towards the nucleus than commonly. The time of keeping in the dark, prior to fixing, varied from three-fourths of an hour to one and one-half hours. I could not bring the amount of retraction into relation with the time of exposure, except that in general the retinas longest exposed showed the greater amount of retraction.

(d) The tissue underlying the retina is described by former observers (Claus, Schewiakoff, Conant) as composed of nerve-fibers and ganglion cells. I cannot give it any other interpretation, but I must add that the supposed ganglion cells are seen only as nuclei, no cell bodies ever being demonstrable in any of my sections. Conant also recognized no cell bodies. Occasionally, as in Fig. 7, long fibers could be traced for some distance in this subretinal tissue, in some instances quite to or from a visual cell. Pigment was not regularly observed in this tissue, as Schewiakoff describes, and when present I believe it has been dissolved in from the pigmented zone.

(e) Schewiakoff describes the retina (my pigmented and nuclear regions) as composed of spindle-shaped visual cells (my pyramid cells?) alternating with pigmented supporting cells (long pigment cells), with the nuclei of the former lying more centrad than those of the latter. The visual cells are pigmented only at their periphery, or surface, leaving an unpigmented axis, while the supporting cells have pigment throughout their whole substance within the pigmented zone. Distally, the visual cells have hyaline rods, or fibers, which extend into spaces in the vitreous body, and pass through this and the capsule to the lens. The vitreous body is described as homogeneous, except the spaces for the visual rods, and a secretion from the retinal cells.

It will thus be seen that my results are quite different from those just described. I find the vitreous body to be composed of prisms and pyramids with axial fibers, while the long pigment cells (supporting cells of Schewiakoff) are continued into the vitreous body, and becoming narrowed into a non-pigmented fiber,

extend to the lens as described. The prisms and pyramids are, further, the distal continuations of cells whose pigmented and nuclear parts lie in the so-called retina, but which, together with the vitreous body, I have named the retina proper. Conant has so summarily disposed of Schewiakoff's distinction between retinal cells based on pigmentation and location of nuclei, that I need not say more. Schewiakoff's Fig. 18 corresponds to my Fig. 1. In this figure he shows the vitreous body as homogeneous with pigmented areas (my long pigment cells) and with spaces with his visual rods. It is quite evident that his spaces with the visual rods correspond to my lighter areas with central dots; *i. e.* my pyramids of the vitreous body are the same as the spaces shown in his Fig. 18. It is quite evident that Schewiakoff mistook the lighter areas for spaces. That they are not spaces can readily be seen by comparing them with real spaces. It is, of course, possible, too, that the reagents had dissolved the pyramids, leaving only the axial fibers with a little pyramid substance about them, and that this is what Schewiakoff saw. I often found small circular spaces in the centers of the pyramid areas, as also in the prism areas (Fig. 3), which might be taken for hyaline visual rods, fibers, in transverse section, but in such spaces I could usually see a small dot to one side of the space that I take to be the rod (fiber) proper. Fig. 14 also shows such small circular spaces that have very much the semblance of hyaline rods. This figure is a transverse section of the vitreous body of the proximal complex eye, in which no long pigment cells or pyramid cells are present, but it serves well to illustrate the point. The above explanation also accounts for the large size of the visual rods (fibers) in Schewiakoff's figures. That the fibers of the pyramid cells (visual rods of Schewiakoff) do not extend to the lens is quite evident in my Figs. 4 and 7.

Again, since the long pigment cells are often not seen to terminate in a fiber, but a part of the fiber can often be seen in the distal part of the vitreous body and in the capsule, it will be quite readily seen how Schewiakoff should associate his visual rods, or fibers, with these distal parts of the fibers of the long pigment cells and suppose his visual rods to extend to the lens.

Again, since the long pigment cells sometimes cannot be seen to terminate distally in a fiber, while the vitreous body at the same time may be broken away from the pigmented zone (Fig. 4), it is

quite evident how Schewiakoff should have interpreted the parts of the long pigment cells in the vitreous body as conical pigmented caps placed opposite his supporting cells (long pigment cells).

Finally, since Schewiakoff had only twelve marginal bodies to study, and since this tissue is difficult to preserve properly, I do not believe that I am doing Schewiakoff any injustice by explaining away his results as I have done. This fact remains, that Conant and myself agree in all points in which we differ from Schewiakoff.

To Conant belongs the credit of having first demonstrated the prismatic structure of the vitreous body, and he also regarded the prisms as a part of the retinal cells. H. V. Wilson[15, 8b] suggested, however, some years prior to Conant, that the vitreous body might be of a prismatic structure. Conant had evidence also of both the prism and pyramid fibers, as is well shown in his figures of transverse sections but he found his evidence too meager to make any very definite statements. Indeed, Conant concludes that there are three kinds of fibers in the vitreous body and complains of finding but two kinds of cells in the so-called retina (pigmented and nuclear zones) to which to refer them. He saw the pyramids with their axial fibers as lighter areas in transverse sections of the vitreous body (his Figs. 64 and 68, and my Figs. 1, 4 and 7), but suggests that they may be the same as the long pigment cells, the cells having only to project themselves or their pigment in order to become long pigment cells. This suggested to him to preserve material both in the light and in the dark. I do not think Conant's supposition to be a fact, for I find the pyramids in specimens preserved in the light as well as in the dark. It is, of course, possible that the pyramid cells are in a stage of structural transition to the long pigment cells, for, besides their pigmentation, they also have like nuclei. Furthermore, I held for a long time with Conant that there may be only two kinds of cells in the retina, but I soon found the pyramids so definitely shown as to leave no doubt but that they represented a third kind of cell. For me it remained to first definitely see all the fibers in the vitreous body as also the pyramids in sagittal sections.

Conant describes the long pigment cells with their fibers extending between the prisms of the vitreous body quite as I have described, and in this my work is only confirmatory of his. Conant does not, however, describe the several centrad processes of these cells, nor is

he clear that their distad processes extend to the lens, though he speaks of fibers within the capsule.

(f) What, now, is the function of these three varieties of cells of the retina? Schewiakoff regards his visual cells (pyramid cells), as the name implies, as having a visual function. That they have such it seems reasonable to suppose, since they have an axial fiber in their pyramids. If the pyramid cells are visual cells, it appears that the prism cells also are such. Indeed, since these are the only ones present in the proximal eye and the more numerous ones in the distal eye, and like the pyramid cells have an axial fiber in their prisms, it seems that they are the visual cells *par excellence* of the Cubomedusan eye. Also, the analogy between the prisms and pyramids on the one hand, and the rods and cones of the vertebrate eye on the other hand, does not seem to be so far fetched. It may be of interest, here, to briefly consider Patten's theory of color vision.[5b]

The gist of Patten's theory is this: In the eyes of certain molluscs and arthropods, in the parts of the retinal cells corresponding to my prisms and pyramids, he not only finds an axial fiber (or fibers) but finer fibrils that extend at right angles from these axial fibers to the surface of the rods (I shall here, for convenience, call the prisms, pyramids, etc., rods) where they probably become continuous with other fibrils in the surface of the rods. These fibrils from the axial fibers are arranged in superimposed planes, and if I understand rightly, an axial fiber with its radiating fibrils may be compared to the axial wire with its radiating bristles of a brush used for cleaning bottles, provided the bristles of such a brush be arranged in superimposed planes. The lateral arrangement of the fibrils will, of course, be modified according whether a rod is circular, hexagonal, square, etc., in transverse section. It will also be remembered (p. 49) that Patten describes the retinal cells studied by him as composed of twin cells, and he gives the name *retinophora* to a pair. The system of fibers and fibrils in the rods he names a *retinidium*. Centrad the axial fibers are continued past the nucleus as a nerve fiber. The fibrils extending laterally in superimposed planes from the axial fiber of a rod, Patten supposes to be the ones stimulated by the incoming rays of light, the retinophora being so arranged that the light rays entering them are parallel to the axial fibers or perpendicular to the lateral fibrils of the

retinidium. Again, since the rods are usually the shape of truncated pyramids or cones the lateral fibrils, which are perpendicular to the axial fibers, are of different lengths accordingly as they are situated at the larger or smaller end of a rod. Patten assumes similar fibrils to exist in the rods and cones (particularly the cones) of the vertebrate eye, and he thus makes a general application of his theory. He supports himself in this rather sweeping generalization by the claim to have demonstrated the twin-cell nature of the cones in amphibia and fishes.

For illustration, Patten supposes that if red light only were admitted to the retinophora this would stimulate the fibrils near the broader end of the cone (but that all the fibrils of the retinidium would be stimulated a little) and that we would thus have the sensation of red light. Likewise, if violet light only were admitted, the fibrils at the narrower end of the cone would be stimulated, and we should have violet light. Similarly, if light including all the different wave lengths of the spectrum were admitted, all the lateral fibrils would be stimulated and the sensation of white light produced. The method of stimulation need not be that of a vibration of the fibrils.

Certain grave objections may be raised against such a theory, the most serious, perhaps, being the fact that no such fibrils as Patten has described have as yet been demonstrated for the eyes of those animals that we know have color vision. Yet, as a whole, the objections are perhaps no more serious than any that can be brought against other theories of color vision. What Patten's theory does do, —it gives us a definite mechanical basis to work from, and if these fibrils should be demonstrated for the rods and cones of vertebrates, physiologists would then have a mechanical basis for color vision quite as they now have for hearing. As Patten says, the problem is primarily a mechanical one. However, the theory cannot well pass for more than a suggestion, a stimulus for future work, and in this lies its present value.

It is quite evident that my results for the retinal cells of Charybdea are, if any thing, a support to Patten's theory. While I have not been able to demonstrate the fibrils that are the essential to Patten's theory, yet I have demonstrated the axial fibers of the rods, and if these fibers should be continued as a nerve fiber to some central ganglion (as I believe is reasonable to suppose, see p. 47), I

do not see how we can avoid the conclusion that these axial fibers of the prism and pyramid cells are somehow concerned in vision. In Patten's theory these fibers would represent a conducting element, the real sensory element (fibrils perpendicular to these axial fibers) not having been demonstrated by me.

I have recently read in a short review of Patten's theory[9] that the evidence we at present have points to the tips of the cones (vertebrate eye) as being the seat of the sensation of red. This would be exactly the converse of what Patten's theory supposes. Whether or not this objection is a real one, future investigation only can determine.

Hesse[13] regards the axial fibers that he describes for the rods in worms as the primitive fibers of Apathy. In this I agree with him, regarding the axial fibers I have described as "Primitivfibrillen." Further, I believe, if I understand Apathy rightly, that the fibrils described by Patten as extending laterally from the axial fibers correspond to Apathy's "Elimentarfibrillen."

It is the long pigment cells that are the puzzling element. Since there can be little doubt but that these cells can project and retract their pigmented parts (as already described), it would seem that a part of their function is to check the diffusion of light in the vitreous body when exposed to strong light. This function would be quite analogous to that of the pigmented cells of the vertebrate retina, which in light become projected between the rods and cones. Similar observations have also been made on the compound eyes of arthropods by Herrick[10] and by Parker[7], who find that the distal retinula cells of Palaemonetes project themselves distad in the dark, thus surrounding the vitreous cones with a cylinder of pigment, while (Parker) the pigment of the proximal retinula cells migrates centrad and the accessory cells move distad; in light the reverse takes place. Other observations of this kind are not wanting for crustacea, insects and arachnids. To my knowledge, the pigment changes that I have described are the first of their kind for medusae.

I suggested while describing the capsule, that the lens might be adjustable. That the fibers of the long pigment cells extend to the lens is my principal reason for this. May these cells not represent ganglion cells and their distad fibers nerve fibers? That they are not sensory (*i. e.* are stimulated by light waves) seems to be suggested by their not having any axial fiber and in having several centrad pro-

cesses. These facts suggest that they are not sensory but the center of a reflex mechanism.* When the sensory cells proper are stimulated, the impulses are conducted centrad into some nerve center (it may be the nerve tissue underlying the retina, or other nerve centers such as the two groups of ganglion cells in the upper part of the club, or the radial ganglia) from which center, again, impulses return over fibers leading to the long pigment cells causing them to project their pigment, and conducting the impulse to the lens, to produce a change in its adjustment. Since these cells are not so numerous as the prism and pyramid cells taken together, but in turn have a number of processes continued centrad (the sum of which processes approximates the number of sensory cells, prism and pyramid cells) it appears that these cells are admirably adapted to function in just such a mechanism as I have described,—each long pigment cell serving a number of its immediate neighbors.

Further, we may conceive each of the centrad processes of the long pigment cells as receiving a fiber from one of the sensory cells directly as well as indirectly, as just described. While I have been able to demonstrate only a single centrad process for the sensory cells (prism and pyramid cells), yet this does not exclude the possibility of a nerve fibril passing out from such a centrad process to one of the processes of the long pigment cells, and it seems possible that this constitutes the reflex mechanism. That nerve fibrils ramify in ganglion and sensory cells, and may even leave these cells to join those of other cells, has been well demonstrated by Apathy,[6] so that my finding only a single process of the visual cells leading centrad without giving off lateral fibers cannot be a serious objection. Again, fine nerve fibers coming off from the main centrad process of sensory cells in medusae have been figured by other observers, among whom I mention the Hertwigs. Careful macerations at the seashore would probably demonstrate them for Charybdea.

Hesse thinks that the eyes of the Alciopidæ are adjustable. He

*It may be objected that my criterion, the presence of axial fibers, is not necessarily characteristic of visual cells. However, the great general occurrence of such axial fibers (Patten,[5] Grenacher,[16] Schreiner,[12] Hesse,[13] myself, in simple complex eye, see below, and perhaps others) in eyes in which the retina has only one kind of cells, would seem to indicate that they are quite characteristic of visual cells. Note again that in the proximal eye of Charybdea there is only one kind of cells and with axial fibers.

describes what he supposes to be muscle fibers just exterior (distal) to the lens, and believes that a contraction of these fibers would have the effect of forcing the lens nearer the retina, or *vice versa*. His supposition, like mine, needs experimental verification. Hitherto the only instance known of accommodation in the eyes of invertebrates was that described by Beer[17] for Cephalopods.

The Proximal Complex Eye.—With four exceptions, the description and discussion given for the distal complex eye also holds good for the proximal complex eye (Fig. 13). The four exceptions are: the absence of a capsule to the lens; the absence of the long pigment cells; the absence of the pyramid cells; and the different relative position of the lens and retina. This eye, then, has a cornea continuous with the epithelium of the sensory club, a lens, in structure and probable origin quite like that described for the distal complex eye, and a retina of prism cells with axial fibers for the prisms. Since Conant[8b] has described this eye quite fully, and discussed Schewiakoff's conclusions at length, I shall be brief. Suffice it to say, that Schewiakoff describes two kinds of cells (supporting cells and spindle-shaped visual cells) for the retina of this eye just as he described for the distal complex eye. The vitreous body he likewise describes as being homogeneous and with spaces for the visual rods (fibers) of the visual cells. It is evident that Schewiakoff has interpreted the structure of this eye from analogy with his results on the distal complex eye. Claus likewise has described two kinds of cells for the retina, and the vitreous body as homogeneous. Conant and myself find only one kind of cells in the retina of this eye. The pigmentation that Schewiakoff describes for the vitreous body I believe to have been dissolved in from the pigmented zone of the retina, for I find no regular pigmentation in the vitreous body. Haake's observation, previously noted (p. 42), applies also to the proximal complex eye.

Conant's evidence for the axial fibers of the prisms was clearly insufficient, so that he did not in this respect complete his Fig. 69. I republish this figure with the prism fibers drawn (Fig. 13).

Since the long pigment cells are absent my reasons for supposing the lens of this eye to be adjustable vanish.

Finally, a word on the origin of the lens and the relative position of the lens and retina. The lens and retina in this eye

are evidently not developed from an outer and an inner half, respectively, of the invaginated and pinched-off lens-retina sphere (as is true for the distal complex eye) but from proximal and distal halves respectively. It is also quite easy to understand the connection of the lens in this eye with the supporting membrane. Since the cells of the ectoderm of the club can in many instances be seen to extend to the basement membrane, or supporting lamella, the cells of the lens, which arise from the ectoderm, simply remain in connection with the basement membrane, this becoming thickened to form a support for the lens. That the lens of the distal complex eye has lost its connection with the basement membrane is evidently due to the fact that the lens is formed from the outer half of the lens-retina sphere. The cells of the lens are by this so far separated from the basement membrane as to lose their connection with it. Schewiakoff also notes the fact that the lens and retina of the proximal complex eye are developed from proximal and distal halves of the lens-retina sphere. He further supposes that the portion of the basement membrane that acts as a support to the lens takes the place of the capsule in the distal complex eye. This latter supposition I do not think probable, since the supporting lamella does not form a distinct covering to the lens on its retinal side.

The Simple Eyes.—Since the shape and position of these eyes have already been described (Claus, Schewiakoff, Conant), I shall not tarry long in this respect. Speaking generally, these eyes are flask-shaped (Fig. 12), the proximal pair quite so, while the distal pair are drawn out in the transverse diameter of the club. These eyes are invaginations of the surface epithelium and the shape of the cells lining these invaginations is quite like that of the epithelial cells, except that their distal portions (bordering the lumen of the invagination) are heavily pigmented. The proximal walls (Fig. 12, left side) of the distal pair are heavier pigmented than the distal walls and the proximal pair of eyes. Schewiakoff calls attention to this point. The pigmentation is, furthermore, not only heavier, but the pigmented portion of each cell is much longer in the proximal walls of the distal eyes (indeed, the cells are longer) than in the distal walls. The significance of this I do not understand. Indeed, I am inclined to believe that in life all these eyes are pigmented quite alike and that it is the reagents used that alter or dissolve the pigment in

certain places. Yet, the fact that the cells of the proximal walls of the distal eyes have their pigmented portions nearly double the usual length, shows some deeper significance.

I also note here the small secondary, non-pigmented invagination into the tissue of the clubs from each of the distal simple eyes. Schewiakoff describes this invagination, and it extends in a proximal and dorsal direction (dorsal-side of club opposite complex eye) from the dorsal sides of the distal simple eyes. The cells of these invaginations are not pigmented, but quite like the other pigmented cells in shape, and like these with distal flagellate fibers. I do not see the necessity of assuming, however, that these secondary invaginations are the real sensitive parts of these eyes, while the pigmented parts serve as an iris, as Schewiakoff does in his general discussion.

The histological structure of both pairs of simple eyes is the same. Sections and macerations give me evidence of only one kind of cells, all pigmented alike (except, of course, the non-pigmented secondary invaginations just noted). The cells in these eyes are very closely crowded so that their nuclei lie at several different levels. That they all extend to the lumen of the eyes and are all pigmented could be demonstrated with certainty in many sections, when some of these cells whose nuclei lay most centrad could be followed with the greatest nicety to the lumen (Fig. 12). Macerations (Figs. 8, unlettered cells 21) also show cells with very long cell bodies pigmented at their distal ends and occasionally with a distal process or fiber. While there are, therefore, spindle-shaped cells found, yet they are in every other respect alike, and their differences of shape and position of nuclei are simply the result of crowding. There is, therefore, no evidence of supporting (pigmented) cells and spindle-shaped visual cells (pigmented only externally) as Claus and Schewiakoff have described and which Conant and myself cannot corroborate.

Distally, the retinal cells of the simple eyes have each a fiber (flagellum) that extends into the lumen (Figs. 12, 15, 16, 21). Each flagellum has a dumbbell-shaped basal body just on its entrance into its cell quite like the basal bodies described for the visual cells of the complex eyes (Fig. 12, part left unpigmented). Each flagellum, or fiber, can usually be seen to extend into the cell. In one series I found appearances like Fig. 16, which is a drawing of a part of a section through one of the proximal simple eyes. This section is

quite in the angle between the proximal complex eye and the group of network cells in the upper part of the club. In this series I could very definitely trace the distal fibers of the retinal cells centrad, past the nucleus and into the subretinal nerve-tissue. These fibers could be so easily followed that no doubt can exist as to the fact noted. It thus appears that the axial fibers just described pass centrad through the cells and are continued as nerve fibers. On the evidence of such sections as Fig. 16 I have indicated these fibers as extending centrad through their cells. The lumen of the simple eyes is filled with a homogeneous vitreous secretion. This is often incomplete in some parts; occasionally the secretion shows a formation of globules, but all this I believe to be due to the action of reagents. Indeed, I have found simple eyes in which hardly any secretion was present, while others showed an almost completely filled cavity. In that portion of the vitreous secretion just outside the mouth of the distal eyes I occasionally found numbers of very darkly staining granules. I suspect that these are either bacterial or algal organisms.

As already noted, Claus and Schewiakoff describe two kinds of cells for the retinas of these eyes which neither Conant nor myself can demonstrate. Further, I believe I have shown that only one kind exists. If any doubt should still exist, a section like Fig. 25 (which is from the epithelium of the club, but similar smaller areas with central dots could often be demonstrated in transverse sections of the retinal cells of the simple eyes) I believe should be convincing. Schewiakoff further describes flagella for the retinal cells (his visual cells) of the simple eyes quite as I have described them for all the cells. The pigmentation that Schewiakoff mentions as occurring in the secretions within the lumina of these eyes I believe to have been dissolved in from the pigmented zones. I find no definite pigmentation in these vitreous secretions. These secretions are evidently products of the retinal cells and have been so regarded by former observers.

Lithocyst and Concretion.—The cavity filled by the concretion is lined in places by a single layer of cells, two of which are shown in Fig. 7. This fact has been noted by both H. V. Wilson and Conant. Such cells are evidently remnants of the cells that formed the concretion. The supporting lamella completely surrounds the cavity of the concretion.

The concretion filling the lithocyst has the shape of a hemiprolate spheroid cut in the plane of the axis of revolution. Whether it is of endo- or of ectodermal origin, I believe developmental studies only can determine. Tests made in the Chemical Laboratory show the presence of calcium sulphate with perhaps a very small trace of phosphate.* Nitric acid slowly dissolves these concretions, but I believe Claus was mistaken when he said that they dissolve with an evolution of gas. I watched them dissolve under the microscope, and never could see the least bit of gas formed. If Claus's observation is correct, then the composition of the concretions of C. marsupialis is different from that of the concretions of C. Xaymacana. The concretions, further, were dissolved out of the material preserved in formaline and in osmic acid solutions. For dissolving them in situ I used either nitric or hydrochloric acid, or both. A slight husk remains after all the lime is dissolved.

The Epithelium of the Clubs.—The epithelium is thickest on the dorsal side of a club. The thickening here, as in several other places, seems to be due to a crowding of the cells, in consequence of which the nuclei come to lie at different levels, but I believe that all the cells quite reach the surface. The cells with their nuclei nearest the surface are pyramidal in shape, with the bases of the pyramids toward the surface, while those cells whose nuclei lie deeper (where several layers of nuclei occur) may be spindle-shaped (Figs. 12, 23, 24, 26). Centrad these cells are continued into a single process, which often seems to extend to the basement membrane (Figs. 7, 12, 13, 23, 24). Where the epithelium covers the region of the concretion, the cells become flattened and with the long axis of their nuclei parallel with the surface of the club (Fig. 7). The same holds true for the corneal epithelium (Figs. 7, 13).

It is a significant fact that in many places the nuclei form only a single layer, and in such places one cannot speak of spindle-shaped cells. I cannot find any evidence of sensory and supporting cells as Schewiakoff describes. The fact that spindle-shaped cells may exist is simply a physical consequence of their being closely crowded. Conant arrived at the same conclusion.

But I have another and better reason for supposing the existence

*Mr. J. C. Olsen, of the Chemical Laboratory, kindly made these tests for me.

of only one kind of cells in the epithelium. In a tangential section taken just through the tips of the epithelial cells (Fig. 25) I find polygonal areas with a central dot. This section does not at all agree with Schewiakoff's Fig. 8, in which he figures two kinds of cells. In Fig. 25 there can be no evidence of two kinds of cells, unless both kinds have like flagella, for these dots are the transverse sections of flagella continued within the cells (Fig. 26).

The epithelium, then, is flagellate, a flagellum to a cell. Whether there are flagella on the epithelium covering the region of the concretion, I could not determine. But I believe that in all other parts, excepting, of course, the corneas, it is flagellated. The fibers (flagella) of the simple eyes are evidently the flagella of the invaginated epithelium. Each flagellum has a basal body, and I could in many instances determine that it was dumbbell-shaped (Fig. 12). This fact was not always evident, however, and it was only occasionally that I felt sure of it. Often the flagella showed only a general thickening within the cells (Fig. 26) while, again, the thickening (basal body) might be quite localized near the surface of the cell. Each flagellum extends into its cell, and occasionally I could trace one clear past the nucleus into the subepithelial nerve-tissue (Fig. 26), just as I did for the axial fibers of the retinal cells of the simple eyes. In those instances in which I could do this, the fibers could so clearly be traced that little if any doubt can exist. I have thus made bold and have drawn the flagella as continued through their cells into the subepithelial nerve-tissue for all the cells of the epithelium of Fig. 12.

A word on the epithelium covering the network cells of Fig. 13. Conant and Schewiakoff here describe fibers from the supporting lamellæ that pass in bundles in among the network cells. These fibers are supposed to be a part of the supporting lamella which reaches out to be a support for the epithelial cells. (Schewiakoff also describes similar fibers for other parts of the epithelium.) Now, as Conant himself shows in Fig. 13, these coarse fibers are not of the same consistency and staining capacity as the supporting lamella. I found them to stain just like the intracellular parts of the flagella or like the central continuations of the axial fibers of the cells of the simple eyes. I could, also, occasionally trace them to the surface of the epithelium, and beyond, when they became continued as short blunt processes or flagella (Fig. 13). I, therefore, conclude that they are sensory fibers like those I have described for the other epithelial

cells. Yet, that they pass to the supporting lamella, just as Conant shows in Fig. 13, would seem to indicate that they are fibers from the supporting lamella or processes of the epithelial cells. While this stands as an objection to their being sensory fibers, yet I cannot explain away their being continued distally as a flagellum, except I assume this continuation to be an artefact. This does not seem probable. Perhaps they serve both purposes; namely, that the cell body with its axial fiber is continued to the supporting lamella, the cell proper ending there, while the axial fiber is continued as a nerve fiber. I believe this to be the proper explanation.

The epithelium of the peduncle is quite like the epithelium of the club just described. Sections through the tips of the epithelial cells of the peduncle and also sections sagittal to the axis of these cells give sections like Figs. 25 and 26. I, therefore, conclude that this epithelium is a sensory flagellate epithelium like that of the clubs. Nerve tissue and unstriped muscle fibers underly the epithelium of the peduncles. Claus and Conant also describe a small ventral endodermal tract of nerve tissue, which according to Conant is connected with the endodermal nerve tissue found in the region of the radial ganglia.

To sum up, the epithelium of the club and the peduncle is a flagellate sensory epithelium whose flagella are continued through the cells as nerve fibers into the nerve tissue below. *A priori*, judging from the mass of nerve tissue underlying the epithelium, we should expect the epithelium to be one strictly sensory. What sense it serves is difficult to surmise. In the physiological part of this paper I suggested that it might be tactile, serving in connection with the lithocysts in giving the animal sensations of space relations.

Claus mentions having seen patches of flagella on the epithelium of the clubs. Schewiakoff supposes that his spindle-shaped sensory cells have only a single flagellum, while his supporting cells have many cilia. In the latter supposition he was evidently mistaken. Conant (from an unpublished note) saw the flagella of the epithelium on the living object and does not think that there could be more than a single one to each cell. He also concludes from living specimens squeezed out under a cover-glass, that there is only one kind of cells in the ectoderm.

Cilia and flagella extending into the cells to which they are attached are described by a number of observers.

I shall not endeavor to discuss the subject further, but shall append the literature on the subject that has come to my notice. (See Literature). Some of these observers ascribe a nervous function to these centrad continuations. I am inclined to believe that they represent the primitive fibrils of Apathy, whether the cilia or flagella are motile or sensory. I should mention, however, that Apathy has traced the "Primitivfibrillen" to be continuous with cilia, and also traces them into the sensory rods of the sensory cells in the sense organs of leeches. Eimer also describes cilia as continued centrad.

The Network Cells and the Multipolar Ganglion Cells.—Conant is the first to accurately describe the true structure of the network cells (Fig. 13) that fill the upper part of the club between the proximal complex eye and the attachment of the peduncle. I cannot add anything to Conant's description. As their name implies, they are filled with a coarse network-like structure with a central nucleus and nucleolus. Schewiakoff erroneously described them as ganglion cells and Claus as supporting cells. I have sometimes thought that they are not made up of a network, but of a vesicular structure; *i. e.* the network we see is really produced by the sections of planes that intersect to form little polyhedral cavities. I could not, however, satisfy myself on this point. I further saw similar but smaller cells, with a finer network, disposed in small groups laterally and distally from the attachment of the peduncle to the club.

What the function of these network cells is can only be guessed. In size and shape they somewhat resemble some of the cells found in luminous organs. Conant, however, nowhere mentions that Charybdea is luminous.

Lateral to the larger group of network cells lie two groups of large multipolar ganglion cells (a group on each side). Claus describes these cells, but Schewiakoff does not specially note them, and evidently considered them a part of the network cells, which he erroneously described as ganglion cells.

The Nerve Tissue.—I cannot add anything new on this. It consists of fine fibers and ganglion cells, quite as described by Claus, Schewiakoff, and Conant, and fills the club between the ampulla and the epithelium, except the spaces occupied by the eyes, lithocyst, and network cells. It is likewise present under the ectoderm of the

peduncle, where also a small tract is found under the endoderm. (See preceding head, or Claus[3], and Conant[8b]). As already noted, under the distal complex eye, I find only large nuclei to represent the ganglion cells. By saying this, however, I do not wish to dispute their ganglionic nature. The large multipolar ganglion cells I have noted under the preceding topic.

The Supporting Lamella.—The supporting lamella is a continuation, through the peduncle, of the jelly of the bell. It completely surrounds the ampulla and the lithocyst, and also forms a partition between them, so that, as already noted, the lithocyst becomes completely surrounded by it. It also sends a partition ventrally between the complex eyes (Figs. 7, 13). Its thickening to form a support for the lens of the proximal complex eye has already been noticed. I shall limit myself in the discussion of the supporting lamella to the above short resumé, since Schewiakoff gives further detail.

The Endothelium of the Ampulla and the "Floating Cells."—The ampulla is lined by a secreting epithelium. This is shown by the large masses of a secretion within the bases of the cells, and by smaller masses scattered in the central and more distal parts (Figs. 7, and 27, lower half). The section of the cells is such in Fig. 7, that the bases of some (those nearest the supporting lamella) are taken, the central nuclear region of others, and the tips of those farthest from the supporting lamella. The section may be said to be taken diagonally through the bases and central parts of some of the cells, but owing to the curvature of the ampulla wall, through the tips of others. The secretion is a colloid substance, staining yellowish gray with iron-hæmatoxylin, blue with Lyons blue, and reddish with borax-carmine. Sometimes darkly staining rods and fibers of unknown origin could be seen within the larger masses of the secretion (Fig. 7). These rods and fibers could also be seen in spaces within the cells, from which the secretion had evidently been dissolved. I think there can be no question but that the masses described are a secretion. Many series, however, do not show it; indeed, an examination of Conant's slides gave me little evidence of a secreting function, though I could demonstrate it in his sections both within the endothelium and also the floating bodies. The

presence or absence of this secretion is evidently correlated with the feeding habits of the animals, or else it would be more generally present.

The endothelium is thickest (the cells are longest) in the upper part of the ampulla where the supporting lamella approaches the lens of the proximal complex eye, and in the lower portion of the ampulla (Fig. 7), in the angle between the concretion cavity and the region of the distal complex eye. In general, the cells are longest in the upper part of the ampulla, while in the lower part, especially where they cover the concretion cavity and the dorsal wall, they may be quite cubical instead of columnar. Often they present a vacuolated appearance at their bases (Fig. 27). Claus and Schewiakoff describe and figure this endothelium, but not in detail. No one, to my knowledge, has described this secretory function.

The nuclei of these cells are peculiar. They may contain a network with a nucleus (Fig. 27). Again, they may show evidence of amitotic division (Fig. 20, h, i, j). Indeed, Remak's scheme (Wilson[18] "The Cell," p. 46) can be quite readily demonstrated. It is, however, such dumbbell-shaped, elliptical, or ringed nuclei as seen in Figs. 7 and 20 that are of special interest.

I have spoken of some of these nuclei as dumbbell-shaped, elliptical, or ringed. This is so, however, only in sections. They are really flattened spheres with a rod of tissue, of the same structure as the nuclear wall, stretching between the poles. One may conveniently compare the shape of these nuclei with that of an apple, the core of the apple representing the rod connecting the two opposite flattened or slightly hollowed poles of the nucleus. For convenience I shall call the rod connecting the two poles the axis of the nucleus. The dumbbell or elliptical shape would be obtained by a meridional section through the axis (Figs. 20, a, b, c, e, g, k, l, m, n, o, 7). Likewise a ringed appearance with a central dot would be obtained by a section parallel with the flattened surfaces or perpendicular to the axis (Figs. 20, d, 7). In a section not strictly meridional the axis would be cut as in Fig. 29, a, or not show at all. As nearly as I could determine, the inside of these nuclei is a vacuole, which the axis penetrates.

The walls and axis of these nuclei have the structure of a very fine and dense network that stains very dark with iron-hæmatoxylin. It stains quite like the reticulum of any nucleus, but is very dense,

as though all the reticulum of the nucleus had been crowded together at the surface. Judging from appearances like p (Fig. 20), the hollowing out, so to speak, of these nuclei, would seem to be a process of vacuolation, the reticulum becoming crowded aside to the surface. But how, on this view, to account for the formation of the axis, I do not know. Perhaps the axis is formed by a pushing in of two opposite poles of a nucleus, the two invaginations meeting and fusing. On this supposition one might expect the axis to be hollow (cylindrical), but I could not determine that it was. Perhaps the centrosphere (or spheres) (see the next paragraph) has something to do with the formation of the axis (Fig. 20, b, g, e, etc.).

In the nuclei of Fig. 20 with the dark outlines, and of Fig. 7 a small reticular body is seen just opposite one end of the axis, or opposite both ends in g. In d (Fig. 20) this body is seen next the axis just below (outside) the hollow cup represented by the hollow ring. In this instance a central granule is seen in the reticular body, as also in c. I take this reticular body to be the centrosphere, and the central granule in c and d the centrosome. In k, l, m, n, and o (Fig. 20), which are from another series, in which the walls of the nuclei did not stain so dark as in the other nuclei of the same figure, a nucleolus could be definitely seen, indeed, sometimes quite perched upon the wall of the nucleus (k, l). In several instances I could see two nuclei, as in o. But besides these nucleoli, I could in several instances see quite definitely a reticular body (centrosphere) opposite the axis (m, n, o) quite as I described for the nuclei with the dark outlines. In a, b, c, d, e and g the nuclei could not be so readily demonstrated, but I could occasionally see a darker stained body as in a, c and g, that I have no doubt is the nucleolus, which here, again, is perched quite upon the surface of the nucleus. This position of the nucleolus is perhaps due to its having been crowded to one side by the nucleus becoming hollow. It is no uncommon thing, either, to find several nuclei in a single cell, sometimes in process of division or just divided as o and e (Fig. 20), also h, i and j. The whole nuclear phenomenon that I have described seems to be one of division. Perhaps it is somehow associated with the giving off of the secretion of the cells, for these nuclei seem to be found in greatest abundance in those cells in which the secretion is most abundant. In Conant's sections I found but little evidence of these nuclear phenomena as also little secretion, which all goes to

show the association of the nuclear phenomenon with the secretion. I have failed to find any descriptions in the literature of nuclei to which I could refer my observations.

The endothelium of the ampulla is flagellated (Figs. 7, 17, 27). It will be seen that there are two slender flagella to a cell. Each pair of flagella has a pair of basal bodies that are longer than thick, and which are continued as a thin fiber towards the nucleus of the cell. That these centrad continuations of the basal bodies extend to or past the nucleus I could not determine. Sometimes the basal bodies with the centrad continuations are pushed quite to one side of the cell (Fig. 27), while in other cells they are applied quite to the distal surface (Figs. 7, 17, 27). Fig. 17, and the part of Fig. 7 that shows these points, are taken just through the tips of the cells. The darker lines within the polygonal areas are the intracellular basal bodies with their centrad continuations, while the thinner lines are the flagella, and are supposed to lie in the plane just below the plane of the figure. In those instances in which the centrad continuations are applied to the distal surface of the cells they could occasionally be seen to bend centrad (Fig. 27b). While these cilia with their basal bodies and centrad continuations are usually separate, as shown in the figures, yet they are at times applied quite closely to each other so that the double nature of the basal bodies and their centrad continuations is not evident. When the intracellular continuations of the cilia become pushed to one side or applied to the distal surface of the cells, I believe this to be due to the turgor of the cells consequent upon the deposition of large masses of secretion within them. But I must add that this explanation is not altogether satisfactory, since in the endoderm cells of the pedalia of both Charybdea and Tripedalia I found like conditions with no evidence of a secreting function. (See below, under tentacles.) No one, to my knowledge, has described the flagellation in detail, although both Claus and Schewiakoff state that the endoderm is ciliated.

The "floating cells" in the stomach pockets and in the ampulla, described by Conant, I believe are in part derived from the endothelial cells of the ampulla. That a portion of them may arise from the ovary, as Conant explains, I do not doubt: I have, further, found a mass of floating cells in a small Charybdea quite as Conant describes for Tripedalia (his Fig. 71). In this Charybdea, however, I could find no traces of any ovary. Conant speaks of larger and smaller floating

cells, and that the smaller ones are also found in the males. This latter fact agrees with what I have suggested, that some of the floating cells arise in the ampulla. My chief reasons for my supposition, however, are the following: I find globules of the secretion of the ampulla cells in some of the floating cells and also scattered loosely among them (Fig. 19). These globules in and among the floating cells have the same general appearance and a similar staining capacity as the secretion in the ampulla cells. Again, in spaces within some of the ampulla cells I find bodies resembling the floating cells with lumps of the secretion within them (Fig. 18). The conclusion, therefore, lies near that some of the floating cells originate within the cells of the ampulla, engulf within them some of the secretion, and are then expelled into the lumen of the ampulla. Better said, perhaps, they represent portions of the ampulla cells with some of the secretion. I also found several instances in which a floating cell had the appearance of being expelled from an ampulla cell. Conant suggests for a similar observation that the cells were about to be swallowed by the ampulla cells. I believe, however, that my finding a secretion similar to that within the cells of the ampulla, in some of the floating cells, as also bodies very much like them and filled with secretion within the ampulla cells, together with Conant's finding floating cells in males, and finally the observation that the floating cells are usually quite dilapidated, never showing a healthy cell structure—all this leads me to conclude that some of the floating cells originate from the ampulla cells, and that they have a nutrient function in distributing the secretion. This is quite the reverse of what Conant supposed,—that they were taken in as nourishment by the ampulla cells. I also find what appears to be a secretion in the endoderm of the tentacles of both Charybdea and Tripedalia, and believe this is another source of the floating cells. (See below, under tentacles.)

I also found other very darkly staining bodies (Fig. 19) both within the floating cells and free in the ampulla cavity, and more numerous in the ampulla cells themselves. This again goes to show that floating cells take their origin from the ampulla cells. What these darkly staining bodies are, I cannot say. Perhaps they are something akin to the "Chromatoider Nebenkörper" described by Lenhossek (L), or they represent another kind of secretion. If these floating cells are derived from the cells of the ampulla, the active

nuclear division within these also receives an explanation. Some nuclear matter can usually be observed in the floating cells.

The Endothelium of the Peduncle.—The endothelium of the peduncle consists of flagellate columnar cells (Fig. 27, upper half). The cells are vacuolated at their bases like some of the cells of the ampulla, and contain a comparatively large nucleus with nucleolus. The flagella are long and slender, quite like those described for the cells of the ampulla, except that there is only one to each cell. The basal bodies of the flagella are of a peculiar shape. They may be described as a bent spindle, continuous at their distad ends with the cilia and at their centrad ends with a fiber that can be traced quite to the neighborhood of the nucleus. I could not trace these fibers into the basal parts of the cells, except in one instance, and I could not be sure of that (Fig. 27a).

Another interesting observation in connection with the basal bodies is that they are bent in one direction on one side of the canal and in an opposite direction on the other side. In Fig. 27, which represents a longitudinal section of the endoderm and the supporting lamella of the dorsal (*i. e.* farthest from the eyes) side of the peduncle, the distal ends of the basal bodies are bent towards the ampulla, while on the ventral side they would be bent away from the ampulla. This seems to suggest that the flagella move the contents of the canal in one direction on the dorsal side of the canal and in an opposite direction on the ventral side. Conant observed in living material that bodies in the ampulla and the canal were moving about, and that bodies within the tentacles were moving in opposite directions at the same time. This last observation and the histological facts just described, I believe, are mutually corroborative. Again, *a priori*, we should expect some such mechanism as the one described to bring about an exchange between the contents of the ampulla and that of the stomach pockets. I have not as yet been able to demonstrate a similar flagellate mechanism in the tentacles. Flagella and basal bodies are present in the tentacles, but I could not determine that the basal bodies had any definite arrangement like that shown in Fig. 27. (See under tentacles.) I may add, yet, that the cells in the canal of the manubrium have cilia, similar to the ones just described, with large basal bodies, and with centrad continuations. Finally, I am not certain but that these cells form buds at their ends quite

like those I describe for the endothelial cells of the tentacles (see below), and that they aid in the formation of the floating cells. I thought I saw such buds just at the entrance of the lumen of the peduncle into the ampulla, but could not find conclusive evidence.

The Tentacles and the Pedalia.—My observations on the tentacles were begun with the object of demonstrating a flagellate mechanism similar to the one described above for the endothelium of the peduncle. While I have failed to demonstrate such a mechanism for the tentacles, yet several interesting points came to my notice. It will be remembered that the tentacles of the Cubomedusæ are not directly attached to the bell, but that a blade-like portion, the pedalium, intervenes between the tentacles and the bell. For figures of the pedalia and the tentacles the works of Haake, Claus, Conant and Maas[22] may be consulted.

The Ectoderm.—The ectoderm of the tentacles is the seat of a number of differentiations. It is quite thick, as the figures (28 and 29) show, and in this respect is very different from the pedalia, on which the ectoderm cells are quite cubical. I found evidence of cilia here and there, but I can add nothing definite about them. Neither can I add any definite statements regarding the ectoderm cells proper, but what I have to say relates to their differentiations.

(a) The *thread cells* are of two kinds, larger ones and smaller ones. This is well shown in Fig. 29, which is part of a transverse section of a tentacle of Tripedalia. Two kinds of nettle-cells are also present in the tentacles of Charybdea, but they were specially well shown in Tripedalia. The structure of these thread-cells seems to be typical, and I have little more to say about them. I wish, however, to call attention to the five or six unstriped muscle-fibers that are attached to their basal lateral parts, and which connect them with the basement membrane (Figs. 28, 29). Claus describes these muscle-fibers and mentions that Fr. Müller has described them before him, but I have not found them mentioned elsewhere in the literature of nettle-cells. Professor Brooks tells me, however, that he has often found them. It would appear from Fig. 29 that they serve to retract the thread-cells from the surface. Claus suggests that the muscles are developed from the cnidoblasts.

(b) The plain subectodermal *muscle-fibers* are of interest. In

Charybdea they lie wholly enclosed within canals of the supporting lamella (Fig. 32, upper part). They run longitudinally, and near the base of each tentacle pass out of their canals and become strictly subectodermal (Figs. 31, 32). This is for Charybdea. In Tripedalia they rarely come to lie in closed canals as in Charybdea. These facts show beyond doubt that these muscles are developed from the ectoderm. Claus has suggested their ectodermal origin, but did not demonstrate it. He also suggested that they become inclosed in canals by the supporting lamella pushing up around them and finally fusing above them. This, I believe, is demonstrated by the conditions in Tripedalia (Fig. 29). Here the canals usually remain open, but occasionally, as in the left-hand canal, one may become completely inclosed. This condition of things suggests the intra-lamellar muscles found in actiniarians. The nuclei found in the canals with the muscle-fibers probably belong to the cells from which the muscles become differentiated. Claus figures these muscle-fibers and nuclei, and it may be added that the supporting lamella he figures, for C. marsupialis, is much thicker than I have figured it for C. Xaymacana and Tripedalia cystophora. The number of muscle-canals also is greater and occupies a much greater depth of the thickness of the lamella. Since Claus gives a figure of a transverse section showing the muscles in their enclosed canals, I have not deemed it necessary to duplicate his figure. In the transition from a tentacle to a pedalium, the muscles are most strongly developed toward and at the edges of the pedalium. This is true for the pedalia in general, and accounts for the readiness with which they can be bent inwards, as noted in the physiological part of this paper.

(c) I have found a single *ganglion-cell* among the cells of the ectoderm of the tentacles. This showed so plainly that I have figured it (Fig. 28). Other ganglion-cells no doubt exist, but could probably not be distinguished from other cells. In its position in Fig. 28 it appears to be associated with the nettle-cell shown just above it. Its position is very much the same as that figured by Lendenfeld (25a).

The Endoderm.—The cells of the endoderm of a tentacle are long and quite slender (Fig. 31). At their bases they are vacuolated quite like the cells of the ampulla and the canal of the sensory clubs. They contain a well-formed nucleus with a nucleolus. In their distal half small light bodies with a dark center are very evident. These bodies are evidently a secretion.

Another peculiar phenomenon presents itself in these cells. The distal part of each cell becomes separated off from its body by what appears to be the formation of a transverse cell-wall (Fig. 31, c–d). I have found the ends of these cells quite separated off in some series. The formation of the walls seems to begin as a thickening at the sides of the cells, and a section through this region, transverse to the cells, would appear like Fig. 30. The dots in the centers of the polygonal areas of this figure are the centrad continuations of the cilia to be described below. As already remarked in describing the endoderm of the ampulla, I believe we here have another place of origin of the "floating cells." The secretion just described moves into the distal parts of the cells prior to their separation (Fig. 31). In some series I could see these secretion bodies much more numerous within the distal ends of the cells than in Fig. 31.

As will be seen in Fig. 31, each of the endoderm cells of the tentacles has a flagellum that extends into the lumen of the tentacle. Each flagellum has a thickening just within its cell, which may be regarded as a basal body. From this basal body, again, a small fiber extends centrad into each cell. It does not appear that the flagella are thrown off with the distal parts of the cells; at all events, I never found them connected with any of the floating cells except in a few doubtful instances.

What I have said for the endoderm of the tentacle of Charybdea applies equally to Tripedalia.

Claus, in his figure of a transverse section of a tentacle of C. marsupialis shows the endoderm as cubical. I cannot explain why there should be such a difference between the endoderm of the tentacles of *C. marsupialis* and that of the tentacles of *C. Xaymacana* and *Tripedalia cystophora*. Claus does not describe the endoderm in detail.

The endoderm cells of the pedalia of both Charybdea and Tripedalia are cubical and possess flagella, basal bodies, and centrad continuations, quite like those I have described for the endoderm cells of the ampulla. The double nature of the basal bodies and the centrad continuations is, however, not so evident. A secretion I did not find. Histologically, therefore, the endothelium of the pedalia corresponds rather with that of the ampulla, and that of the tentacles with that of the peduncle of the clubs.

SUMMARY.

The most important results in the histological part of this paper relate to the structure of the retinas of the eyes of the sensory clubs.

The retina of the distal complex eye is composed of three kinds of cells: two kinds of sensory cells (the prism and pyramid cells), and the long pigment cells (Figs. 1–9). The prism and pyramid cells have each an axial nerve fiber in their prisms and pyramids respectively. These fibers I could, however, trace only to the neighborhood of the nuclei. But since I could trace similar fibers in the retinal cells of the simple eyes (Fig. 16) past the nucleus into the subretinal nerve tissue, I believe that the axial fibers in question also extend centrad as nerve fibers into the subretinal nerve tissue. Other observers also figure such fibers as extending centrad as nerve fibers. The axial fibers of the prism cells have each a dumbbell-shaped basal body at their entrance into the pigmented part of a cell. The evidence for a body of such shape in the pyramid cells was not conclusive, though a basal body for the axial fiber exists. The long pigment cells project or retract their pigment in light or darkness respectively and thus seem to serve to check the diffusion of light in the retina. I have also supposed that these cells may serve for conducting impulses to the lens, and that the latter is adjustable.

The proximal complex eye (Fig. 13) has only the prism cells present in its retina, and not two kinds of cells as Schewiakoff has described (see text, pp. 53, 60, 63) for all the eyes.

The simple eyes (Fig. 12), two on each side of a club, four in all, also have only one kind of cells in their retinas, and each cell has a flagellum extending into the vitreous secretion of the lumen. These flagella could be traced centrad as a nerve fiber (Figs. 12, 16). Similarly, a nerve fiber could be traced centrad from the flagella of the epithelial cells of the clubs. Dumbbell-shaped basal bodies for the flagella of the simple eyes could also be demonstrated, but the evidence for this in the epithelial cells of the clubs was not so satisfactory.

Other points of interest are: A secretory epithelium lining the ampulla of the clubs, and a somewhat similar epithelium lining the canals of the tentacles (Figs. 7, 27, 31); the partial origin of the "floating bodies" in the canals of the clubs and tentacles and the stomach pockets from these epithelia (Figs. 18, 19); two flagella to

each cell of the endothelium of the ampulla and of the pedalia (Figs. 7, 17); the peculiar nuclei in the endothelial cells of the ampulla (Fig. 20); the longitudinal muscles of the tentacles being completely inclosed within canals of the supporting lamella, but near the base of a tentacle becoming subectodermal. This demonstrates their ectodermal origin. In Tripedalia it is seldom that any of these muscles become enclosed as in Charybdea (Fig. 29).

If to the reader my results seem to embody a somewhat heterogeneous detail, he must remember that the work consists partly in corroborating and partly in supplementing the work of previous observers, and that, in general, histological detail does not usually make the most readable paper.

Biological Laboratory,
Johns Hopkins Univ., May, 1899.

LITERATURE.

LITERATURE REFERRED TO IN THE SECTION ON PHYSIOLOGY.

I. Romanes, G. J. a. '75, '77. The Locomotor System of Medusæ. Philosophical Transactions. London. Vol. CLXVI, pt. 1. Vol. CLXVII, pt. 2.

b. '85. Jelly-fish, Star-fish and Sea-urchins. London.

II. Murbach, Louis. '95. Preliminary Notes on the Life-history of Gonionemus. Journal of Morphology. Vol. XI.

III. Hesse, R. '95. Über das Nervensystem und die Sinnesorgane v. Rhizostoma Cuvieri. Zeit. Wis. Zool., B. LX.

IV. Eimer, Th. Zoologische Untersuchungen. '74. Würzburg Verhandlungen. VI. Bd.

V. Haeckel, E. '79. Monographie der Medusen. Jena.

VI. Berger, E. W. '98. Abstract of Dr. F. S. Conant's Notes on the Physiology of the Medusæ. Johns Hopkins University Circulars. Vol. XVIII, No. 137.

VII. (See also 8, below.)

LITERATURE REFERRED TO IN THE SECTION ON HISTOLOGY.

1. Carrière, J. '85. Die Schorgane der Thiere. München u. Leipzig.

2. Haake, W. '87. Scyphomedusen des St. Vincent Golfes. Jen. Zeit. f. Naturwis., Bd. XX., pp. 596–597, 602–604.

3. Claus, C. '78. Über Charybdea marsupialis. Arb. aus dem Zool., Inst. Univers. Wien., Bd. I.

4. Schewiakoff, W. '89. Beiträge zur Kenntniss des Acalephenauges. Morph. Jahrb., Bd. XV, H. 1.

5. Patten, William. a. '89. Studies on the eyes of Arthropods. II. Eyes of Acilius. Journal of Morphology. Vol. II.

b. '98. A Basis for a Theory of Color Vision. American Naturalist. Vol. XXXII, No. 383.

6. Apathy, St. '97. Das Leitende Element des Nervensystems u. seine topographischen Beziehungen zu den Zellen. Mitt. Zool. Stat. Neapel., Bd. XII, H. 4.

7. Parker, G. H. '97. Photomechanical Changes in the Retinal Pigment Cells of Palæmonites, and their Relation to the Central Nervous System. Bull. Mus. Comp. Zool. Harvard Coll. Vol. XXX, No. 6.

8. Conant, F. S. a. '97. Notes on the Cubomedusæ. Johns Hopkins University Circulars. Vol. XVII, No. 132.

b. '98. The Cubomedusæ. Memoirs Biological Laboratory Johns Hopkins Univ. Vol. IV, No. 1.

9. A Review of 5b. '99. A Theory of Color Vision. Natural Science. Vol. XIV, No. 85.

10. Herrick, F. H. '91. The Embryology and Metamorphosis of the Macroura (Brooks and Herrick). Natl. Acad. Sciences. Vol. V, p. 454.

11. Hertwig, O. & R. '78. Das Nervensystem und die Sinnesorgane der Medusen. Leipzig.

12. Schreiner, K. E. a. '96. Die Augen bei Pecten und Lima. Bergens Museums Aarbog.

b. '97. Histologische Studien über die Augen der freilebenden marinen Borstenwürmer. Bergens Museums Aarbog.

13. Hesse, R. '99. Untersuchungen über die Organe der Lichtempfindung bei niederen Thieren. V. Die Augen der Polychäten Anneliden. Zeit. Wis. Zool., B. LXV, H. 3.

14. Andrews, E. A. '92. On the Eyes of Polychætous Annelids. Journal of Morphology. Vol. VII.

15. Wilson, H. V. '78. Unpublished Notes.

16. Grenacher, H. '84. Abhandlungen zur vergleichenden Anatomie des Auges. 1. Die Retine der Cephalopoden. Abhandl. der Naturf. Gesellsch. zu Halle. Bd. XVI.

17. Beer, Theodore. '98. Die Accomodation des Auges in der Thierreihe. Wiener klinische Wochenschrift. Nr. 42.

18. Wilson, E. B. '96. The Cell.

19. Berger, E. W. '98. The Histological Structure of the Eyes of Cubomedusæ. The Journal of Comp. Neurology. Vol. VIII, No. 3.

20. Lendenfeld, R. Die Nesselzellen der Chidarier. (Review and bibliography.) Biol. Centralbl. Bd. XVII, Nr. 13.

21. Schneider, K. '90. Histologie von Hydra fusca mit besonderer Berücksichtigung des Nervensystems der Hydropolypen. Arch. Mik. Anat. Vol. XXXV.

22. Maas, O. '98. Die Medusen. (Charybdea arborifera, Systematic.) Mem. Mus. Comp. Zool., Harvard Coll. Vol. XXIII, No. 1.

LITERATURE REFERRING TO THE CENTRAD CONTINUATIONS OF CILIA AND FLAGELLA.

A. Haeckel, E. '72. Die Kalkschwämme. Vol. I, p. 141; Vol. III, Pl. 25, Figs. 3–5.

B. Schultze, F. E. '75. Rhizopodien Studien. V. Arch. Mik. Anat. Bd. II, p. 583.

C. Eimer, Th. '77. Weitere Nachrichten über d. Bau des Zellkerns, nebst Bemerkungen über Wimperepithelien. Arch. f. Mik. Anat. Bd. XIV, Taf. VII, p. 114.

D. Bütschli, O. '78. Beiträge zur Kenntniss der Flagellaten, u. s. w. Zeit. f. Wis. Zool. Bd. XXX, p. 269.

E. Engelmann, Th. W. '80. Zur Anatomie u. Physiologie d. Flimmerzellen Pflüger's Arch. Bd. XXIII.

F. Hatschek, B. '85. Entwickelung der Trochophora von Eupomatus uncinatus. Arb. Zool. Inst. Wien., Bd. VI, p. 139.

G. Heider, K. '86. Zur Metamorphose der Oscarella lobularis. Arb. Zool. Inst. Wien., Bd.VI, pp. 189–194.

H. Schneider, K. C. '92. Einige histologische Befunde an Coelenterata. Jen. Zeit. f. Nat. 27, N. F. 20.

I. Hecht, Emile. '95. Contribution a l'Étude des Nudibranchs Memoirs de la Société Zool. de France. T. 8, Pl. IV, Fig. 45.

J. Minchin, E. A. '96. Notes on the Larva and Postlarval Development of Leucolosolemia variabalis, etc. Proc. R. Soc., London. Vol. LX.

K. Henneguy, L. F. '98. Sur le rapports des ciles vibrales avec les centrosomes. Arch. d'anat. micros., T. 1.

L. Lenhossek, H. '98. Über Flimmerzellen. Anat. Anz. (Supplement.) Bd. XIV.

M. Petre, Carl. '99. Das Centrum für die Flimmer u. Geisel-bewegung. Anat. Anz. Bd. XV, Nos. 14 and 15.

N. See also 6.

REFERENCE LETTERS.

a=flagellum in Fig. 27, that is supposed to extend centrad beyond the nucleus.
b=twin flagella in Fig. 27, of which the centrad continuation is seen applied against the distal surface of the cells and to be continued centrad.
c=capsule of lens.
cf=axial fibers of cells extending centrad.
co=cornea.
concr=concretion cavity.
ec=ectoderm.
en=endoderm.
f=flagella.
flp=distal fiber of a long pigment cell.
fpr=axial nerve fiber of a prism cell.
fpyr=axial nerve fiber of a pyramid cell.
frc=axial nerve fiber of the retinal cells of the simple eyes.
gc=ganglion cells.
ind=impression of the lens probably due to the pressure of weight against the surrounding tissue.
l=lens.
lp=long pigment cells.
m=muscle fibers.
namp=nuclei of ampulla cells.
nc=network cells (Figs. 13 and 16), and nettle cells (Figs. 28, 29).
nf=nerve fibers and tissue.
nlp=nucleus of long pigment cell.
nm=nucleus of muscle cells.
nprc=nucleus of prism cell.
npyrc=nucleus of pyramid cell

nz=nuclear zone.
pr=prism of prism cell.
prc=prism cell.
pyr=pyramid of pyramid cell.
pyrc=pyramid cell.
pz=pigmented zone.
r=retina.
s=secretion in endo. of tent. and ampulla.
sh=shrinkage space.
sec=vitreous secretion in the lumen of the simple eyes.
sla=supporting lamella.
vb=vitreous body or zone.
x=(1) the approximate level at which Fig. 4 should be cut transversely to give Figs. 1 and 3.
(2) the thickening of the supporting lamella in Fig. 13 to support the lens.
*=Point of approximation of cells of lenses in Figs. 7 and 13.

DESCRIPTION OF FIGURES.

ALL FIGURES, UNLESS OTHERWISE STATED, ARE FROM CHARYBDEA.

Fig. 1. This figure represents a transverse section through a portion of the vitreous body of the distal complex eye at about the level x of Fig. 4. Three kinds of areas are seen, namely, the prisms and pyramids with their axial fibers and the distal continuations of the long pigment cells. Towards the lower left of the figure the section is a little more distal than at the right and the transverse areas of the long pigment cells are no more so large as at the right of the figure. The dark granules in the areas of the long pigment cells represent pigment. Camera lucida sketch. ×920. pp. 45, 46, 48, 49, 50, 51, 52, 54.

Fig. 2. This figure is a camera lucida sketch from a section taken transverse through the most distal part of the pigmented zone of a slightly pigmented retina of a distal complex eye. The presence of three kinds of elements is again evident. The dots without the polygonal areas represent the centrad continuations of the axial fibers of the prism cells. The lettering explains the other areas. ×920. pp. 46, 48, 50.

Fig. 3. This is from a section similar to that of Fig. 1, but a little more distal. At the right, the section is more distal than at the left of the figure, in consequence of which the long pigment cells are there taken through their distal fibers. Note the small shrinkage spaces about the axial fibers of the prisms. The white lines bounding the prism areas appear as in nature. The pyramid cells are not shown in this figure. ×950. Camera sketch. pp. 50, 51, 52, 54.

Fig. 4. This figure is from a section taken parallel to the long axis of the cells of the retina of a distal complex eye. It is from a camera sketch, and nothing has been put into the figure except what could be clearly seen. The lateral boundary lines of the prisms are not shown. Note the evidence for the existence of three kinds of cells. ×920. pp. 44–52, 54.

Fig. 5. This figure represents a sagittal section through the nuclear and pigmented zones and the subretinal nerve tissue of a slightly pigmented retina of a distal complex eye, that had been killed in the dark. Camera sketch. The pyramid cells are not shown. ×900. pp. 47, 51, 52, 53.

Fig. 6. These cells are from a preparation by Conant of a sensory club, macer-

ated in acetic acid. Cell a is evidently an iris cell. The others are probably prism cells from the proximal complex eye. ×900. pp. 44, 48.

Fig. 7. In this figure I represent a sagittal section through the distal complex eye. In the middle half of the section, the nuclei, the prism and pyramid cells with their axial fibers, and the long pigment cells with their large distal fibers are all strictly camera lucida sketched. A portion of the pigmented zone has been left unpigmented to better show its structure. At the right and above the concretion cavity is shown a portion of the endoderm of the ampulla. The section is not strictly in a dorsoventral plane of the club, in consequence of which the cells of the ampulla are cut diagonally and through their tips. Note the dumbbell-shaped nuclei of the ampulla cells, as also the masses of secretion. A part of the retina of the proximal complex eye is shown in the upper part of the figure. ×920. pp. 41–54, 63, 64, 68–71.

Fig. 8. These cells are from a macerated preparation. Cells a, b, c, d may be either prism or pyramid cells from the distal complex eye or prism cells from the proximal complex eye. Cells e and f are probably from the right fourth (Fig. 13) of the retina of the proximal complex eye or from the simple eyes. The unlettered cells are probably from the simple eyes. Some of these show a distal process. ×900. pp. 48, 62, 65.

Fig. 9. The cells here figured are long pigment cells from the same preparation as Fig. 6. ×900. pp. 50, 51.

Fig. 10. This drawing shows an end view of a group of prisms from the same preparation as Fig. 6. ×900. pp. 46.

Fig. 11. This group of prisms are from the same preparation as Fig. 6. Two of them are broken off. The fibers seen at the lower end are probably some of the axial fibers. The fiber at the upper end I believe is interprismatic and the distal fiber of a long pigment cell. ×900. pp. 46.

Fig. 12. This figure is a summary of my results on the simple eyes. It is from a camera sketch of one of the distal eyes, but somewhat diagrammatic. The left side of the figure is proximal, the right side distal. ×920. pp. 61, 62, 64, 65.

Fig. 13. Sagittal dorsoventral section of a proximal complex eye. Conant drew and published this as his Fig. 69. Conant's evidence regarding the axial fibers of the prism cells was incomplete; so that, in this respect, he left his figure unfinished. I have drawn in these fibers and republish the figure. At the right of the retina and next the lens (the white space) the vitreous body is incomplete and the fibers from the retinal cells project freely into the space. This part of the retina also remains unpigmented. Like my Fig. 7, this figure evidently represents a section somewhat to one side of a sagittal dorsoventral plane of the club, so that the endoderm cells of the ampulla are cut diagonally or transversely. pp. 41–44, 60, 64–68.

Fig. 14. This is drawn to show how regularly small shrinkage spaces may occur in transverse sections of the vitreous bodies. This figure is from a transverse section of the vitreous body of a proximal complex eye. I believe that these spaces are determined by the axial fibers of the prisms. Prism outlines are not shown. ×950. pp. 54.

Fig. 15. This figure is a drawing of a portion of a transverse section of one of the simple eyes. Note the flagella from the retinal cells. pp. 62.

Fig. 16. The section of the lower left hand corner of this figure is through a portion of one of the proximal complex eyes, and shows the centrad continuation of the axial nerve fibers of the retinal cells. The section is such, that, besides the simple eye, the nuclei of the proximal complex eye (upper part of figure) and two network cells are cut. ×920. pp. 47, 62, 63.

Fig. 17. A transverse section through the tips of the ampulla cells is here shown. To the left is towards the upper end of the ampulla. The basal bodies with the centrad fibers are in the plane of the section, while the flagella are supposed to extend below the plane of the section. ×1350. pp. 71.

Fig. 18. These bodies, from within the ampulla cells, contain some of the secretion of the ampulla cells, and resemble the "floating bodies." ×1350. pp. 72.

Fig. 19. The "floating bodies" here represented are from the ampulla. Globules of a secretion similar to that found in the ampulla cells are seen both within and without the bodies. Note also the two black bodies without the cells and two or three similar ones within the cells. These latter bodies are of doubtful nature. ×1320. pp. 72.

Fig. 20. This figure represents sections of the various nuclei found within the ampulla cells. ×1350. pp. 69, 70.

Fig. 21. These cells are from the same preparation as Fig. 6. They are evidently retinal cells from the simple eyes. The tendency of their pigmented ends to become globular, I believe, is due to their having become isolated before they hardened during maceration. ×920. pp. 62.

Fig. 22. This diagram illustrates the retraction of the long pigment cells. The dotted lines in the vitreous body mark the outlines of the prisms, while the continuous lines represent the axial fibers of the prism and pyramid cells. pp. 45, 46, 48, 49, 53.

Fig. 23. These cells are from the epithelium of a sensory club. They are from the same preparation as Fig. 6. Flagella are not shown. ×900. pp. 64.

Fig. 24. This group of epithelial cells of a club are from the same preparation as Fig. 6. ×850. p. 64.

Fig. 25. This sketch is a transverse section through the tips of the epithelial cells of a club. The polygonal areas are the cells, while the central dots are the centrad continuations (nerve fibers) of the flagella of the cells. ×920. pp. 63, 65, 66.

Fig. 26. The flagella of the epithelium of a club are in this figure seen to extend centrad, some beyond the nuclei. Cell outlines are not shown. ×920. pp. 64, 65, 66.

Fig. 27. The cells of the lower half of this figure belong to the ampulla, those of the upper half to the canal of the peduncle. The right side of the figure is towards the eyes (the ventral side) of the club. Globules of secretion are seen within the ampulla cells, as also a globule without. The ring above the latter globule is probably an empty shell of a floating cell. ×1320. pp. 68, 69, 71, 73.

Fig. 28. This figure is from a transverse section of a tentacle of Charybdea.

The mass with darkly stained granules is the remains of a thread cell. The ectoderm and a small part of the supporting lamella only are figured. Note the large ganglion cell. ×920. pp. 74, 75.

Fig. 29. Part of a transverse section of a tentacle of Tripedalia. The endoderm is not figured. The supporting lamella is seen to be considerably thinner than in Charybdea. Note the subectodermal muscles, as also the muscle fibers to the thread cells. ×920. pp. 69, 74, 75.

Fig. 30. This is a transverse section through the endothelium of a tentacle of Charybdea in the line c d of Fig. 32. The dark lines bounding the polygonal areas are the thickenings of the sides of the walls of the cells in the line indicated. The central dots are the centrad continuations of the flagella. ×920. p. 76.

Fig. 31. This figure is a transverse section through a tentacle of Charybdea at about the middle of Fig. 32, *i. e.* so near to where the tentacle joins the pedalium, that the muscles within the lamella have all come to lie under the ectoderm. The ectoderm is not shown. ×920. pp. 75, 76.

Fig. 32. A longitudinal section through the supporting lamella only, of a tentacle of Charybdea, is here shown. In the upper part of the figure the muscle fibers are seen wholly enclosed by the supporting lamella. In the middle of the figure they are seen to pass out of their canal. In the lower part of the figure, the supporting lamella is seen to bend to the right where it becomes continuous with the lamella of the pedalium. ×920. p. 75.

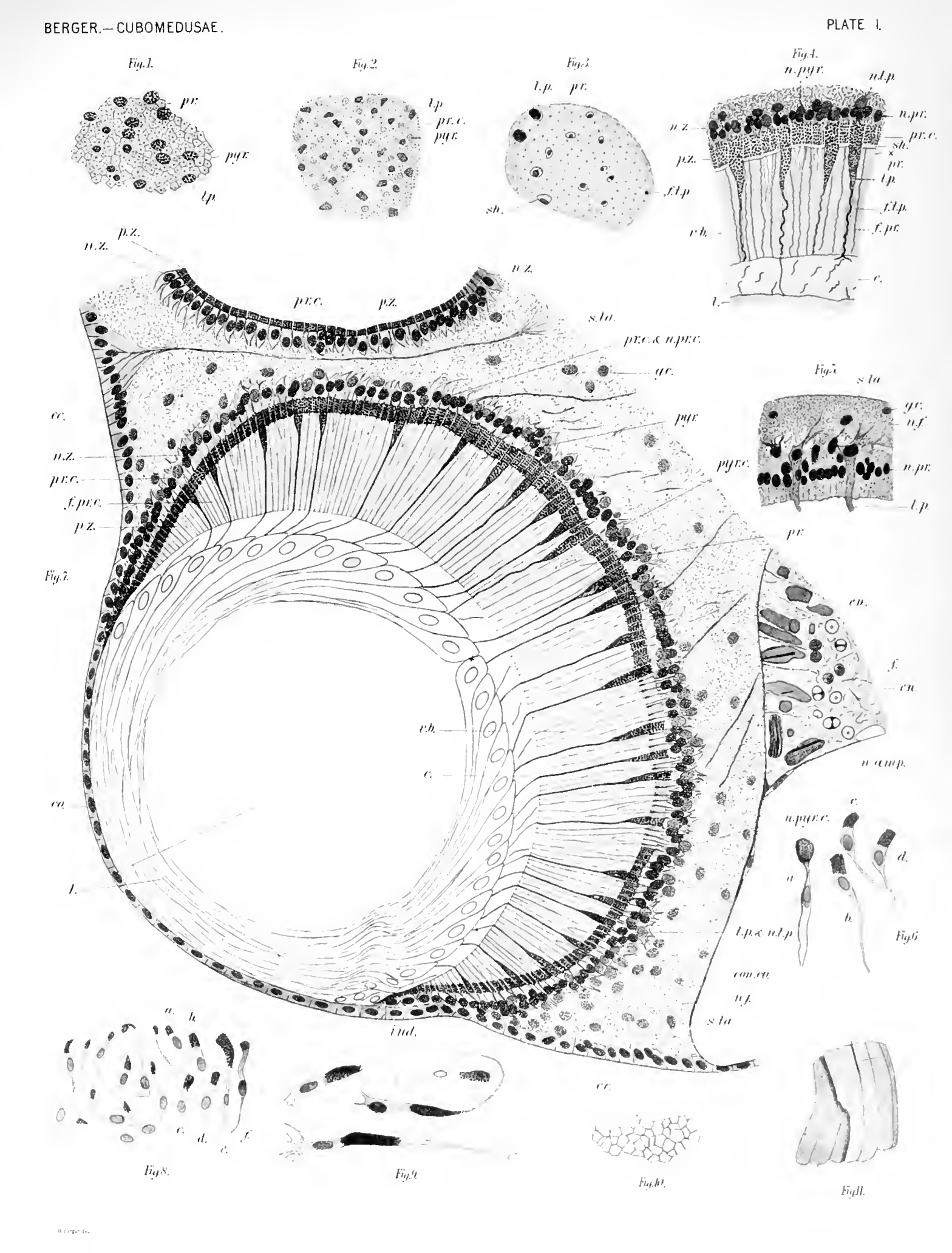
Fig.1.
pr.
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Fig.2.
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Fig.3.
l.p.
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Fig.4.
n.pyr.
n.l.p.
n.z.
n.pr.
pr.c.
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p.z.
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r.b.
f.pr.
c.
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n.z.
n.z.
pr.c.
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s.la.
pr.c. & n.pr.c.
gc.
Fig.5.
s.la
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pyr.c.
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p.z.
Fig.7.
pyr
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l.p. & n.l.p
Fig.6
com.en
n.f.
s.la
ind.
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b.
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d.
e.
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Fig.8.
cc.
Fig.9
Fig.10.
Fig.11.

Fig.12.

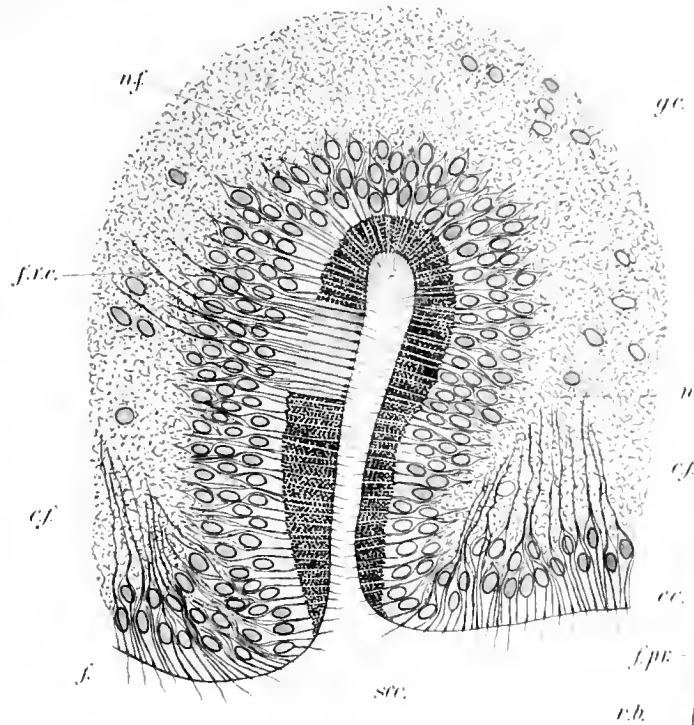


Fig.13.

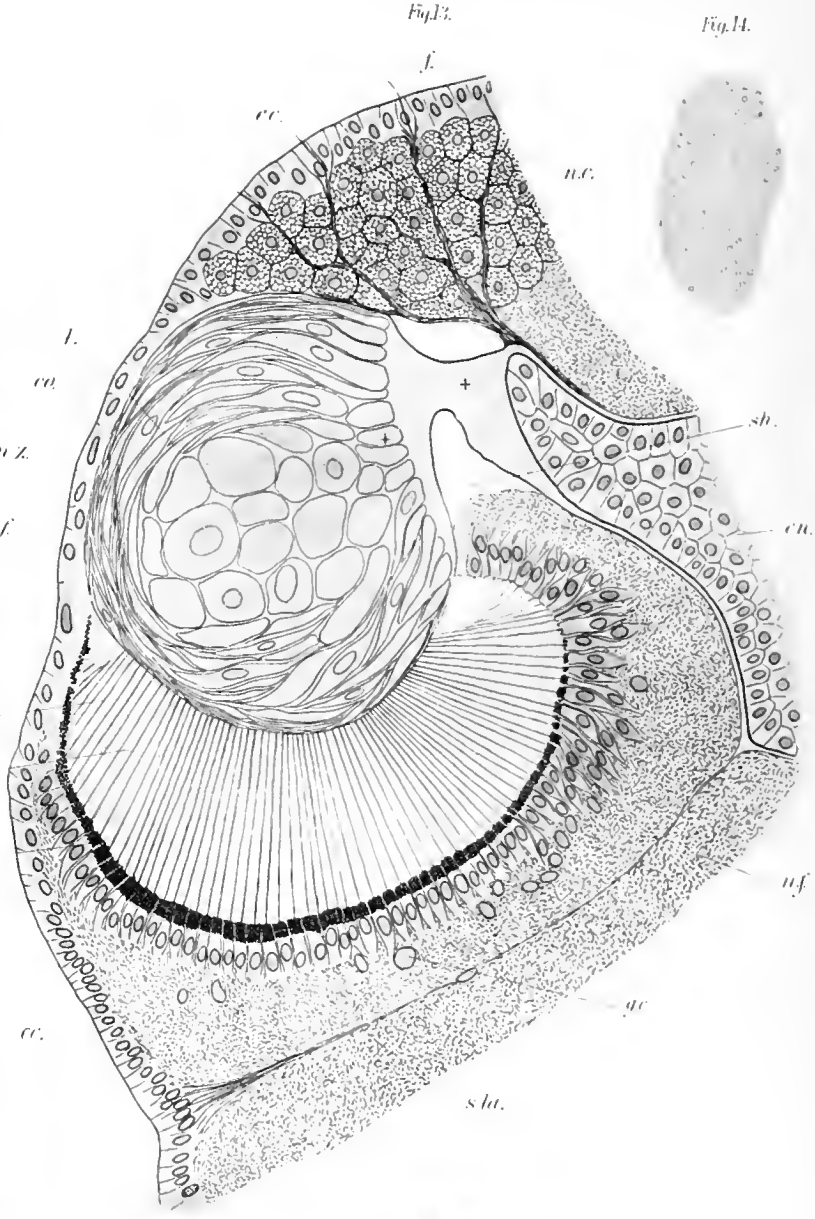


Fig.14.

Fig.15.

Fig.16.

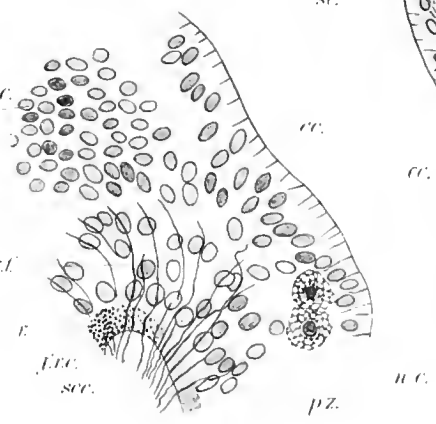
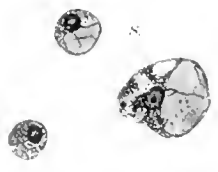


Fig.17.

Fig.21.

Fig.18.



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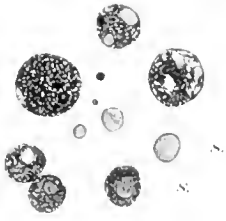

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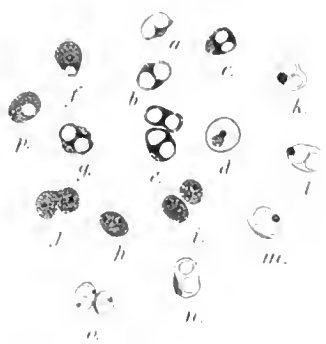

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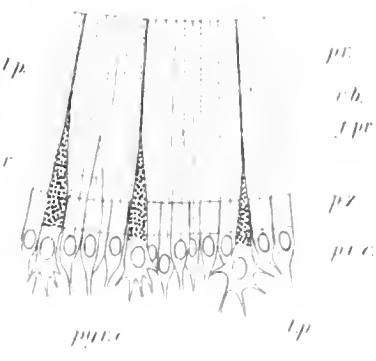

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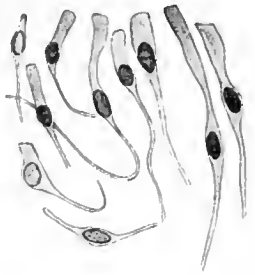
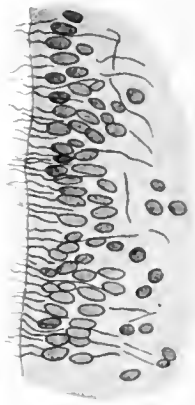


Fig.24.

Fig.25.

Fig.26.



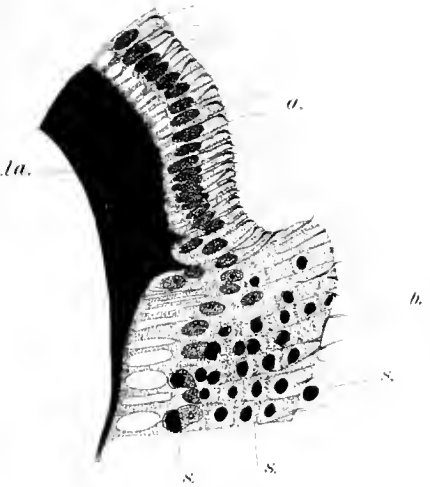
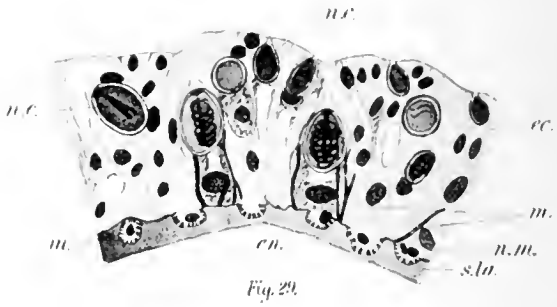


Fig.27.

Fig.28.



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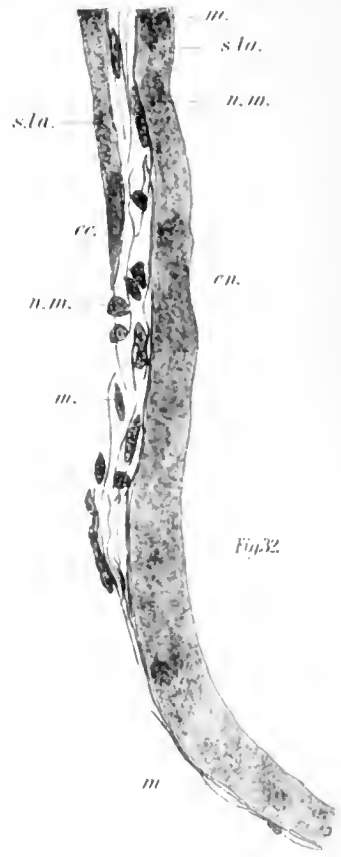

Fig.32.

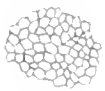

Fig.30.

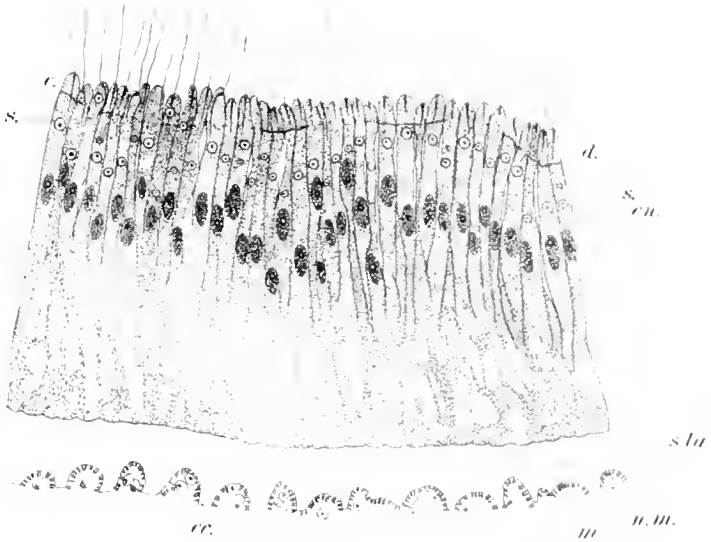

Fig.31.